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I. *On the Development of the Skeleton of the Tuatara, Sphenodon punctatus; with Remarks on the Egg, on the Hatching, and on the Hatched Young.* By G. B. HOWES, LL.D., F.R.S., and H. H. SWINNERTON, B.Sc., Marshall Scholar, R. Coll. Sci. Lond. (From the Huxley Research Laboratory.)

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[With Plates I.–VI. and 18 text-illustrations.]

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I. INTRODUCTION.

ALL work in Reptilian Morphology during the last thirty years has increased the interest attaching to the creation in 1867 by Dr. Günther of the Order Rhyncho-

cephalia, which now, in its extended form, would appear to embrace a series of genera and species occupying a truly central position among the terrestrial vertebrates. Since the publication of Dr. Günther's memoir on *Sphenodon*, the discovery by Baur and others of its vomerine teeth, and by Spencer of its parietal-eye, have more especially increased our knowledge of this remarkable animal beyond that which is ordinary. One of its most distinctive characters is the forward prolongation of the pterygoids to meet the vomers with apposition in the middle line. The mere forward prolongation referred to is a feature already recognizable among the Batrachia and Stegocephalia; but special interest attaches to the median apposition, as there is little room for doubt that in that there lies the clue to the reduction and suppression of the parasphenoid in the ascending series of the Amniota. This important Rhynchocephalian character, long recognized in the Crocodilia and Dinosauria, has during recent years been discovered in the Ichthyosauria¹ and the Plesiosauria² by Lydekker and others, and probably in the Pterosauria by Newton³, and it justifies the conclusion that the living *Sphenodon* may be the sole surviving representative of an early and widely ancestral amniote type. While the recent confirmation by Menzbier⁴ and Pycraft⁵ of Brandt's discovery in 1839⁶ that the Avian pterygoid may reach the vomer, with their further demonstration, that while this is a permanent feature of some Ratitæ and the Tinamous among the higher birds, this Rhynchocephalian character becomes lost during ontogeny under secondary segmentation and co-ossification of parts, as the progressively modified facial skeleton comes into closer relationship with the basis cranii, would seem to indicate an origin for the class Aves from some more primitive reptilian type than might otherwise have been supposed⁷—from something lower than the Dinosauria. Beyond this, Cope in 1870⁸, and Seeley in 1874⁹, have drawn attention to certain Chelonian resemblances in the Rhynchocephalia. In this they have been more recently followed by Boulenger, who regards¹⁰

¹ Lydekker, R.: Brit. Mus. Cat. Fossil Rept. & Amphib., Part 2, 1889, p. 5. Cf. also Baur, G.: Anat. Anz. Bd. x. 1895, p. 456; and (concerning the Rhynchocephalian affinity) Americ. Nat. vol. xxi. 1887, p. 337.

² Lydekker, R.: originally in *Pl. dolichodirus*, ibid. p. 257. Cf. also Andrews, C. W.: on *Peloneustes*, Ann. & Mag. Nat. Hist. (6) vol. xvi. 1895, p. 248, and on "The Structure of the Plesiosaurian Skull" in Journ. Geol. Soc. vol. lii. 1896, p. 246.

³ Newton, E. T.: Phil. Trans. vol. 179 B. 1888, p. 503.

⁴ Menzbier, M. v.: Bull. Soc. Imp. Nat. Moscou (n. s.), tome i. 1887, p. 492.

⁵ Pycraft, W. P.: P. Z. S. 1898, pp. 973-974.

⁶ Brandt, J.: Mém. Acad. Sci. St. Pétersb. (vi.), Sci. Nat. tome iii. p. 81, & espec. pl. xvii. fig. 3 (*Rhyncops*).

⁷ Provided the so-called "hemipterygoid" has the value claimed for it. It must not be forgotten that *Archaeopteryx* appears to have had "abdominal ribs" (Dames, Palæontol. Abhandlg. Berlin, 1884, Bd. 2, p. 144), and that "intercentra" occur in most of the groups of non-Passerres among living birds (Beddard, P. Z. S. 1897, p. 465).

⁸ Cope, E. D.: Proc. Americ. Assoc. vol. xix. 1870, p. 233.

⁹ Seeley, H. G.: Journ. Linn. Soc., Zool. vol. xi. 1876, p. 183.

¹⁰ Boulenger, G. A.: Brit. Mus. Cat. Crocodilia and Chelonian, 1889, p. 1.

"the affinities of the Rhynchocephalia to the Chelonians as at least as great as to the Lacertilia;" while almost the first observation made in the development of the Tuatara was that by Dendy (98, and 99^b. p. 66) of the post-amniotic canal, which, though probably of wide occurrence, was originally discovered¹ and is at present known elsewhere only in the Chelonian, and of the horny "shell-breaker," which, being of the Chelonian type², places *Sphenodon* in sharp contrast to the Lacertilia, which, so far as is known, develop a calcified "egg-tooth."³

Far reaching as is thus the interest arising from a comparison of the recent *Sphenodon* with representative members of the living orders of Reptiles, that with certain extinct orders and suborders other than those already alluded to is even more suggestive. The discovery by Credner in the Permian deposits of Saxony of the assemblage of vertebrate forms he has so aptly termed⁴ the "Eotetrapoda," and more particularly the genus he has less aptly named *Palæohatteria*, has materially lessened the structural gap between the Reptilia and the Stegocephalia; while the description by Lortet, eight years ago, of Rhynchocephalian remains⁵ from the Upper Jurassic of the Rhone Basin which reveal new cranial characters, with that of Crocodilian resemblances in *Champsosaurus*⁶, which, like *Acrosaurus*⁷, is believed to have been aquatic in habit, shows the Rhynchocephalian Order, now all but extinct, to have been in the past extensive and subject to considerable modification. It is now generally conceded that the Anomodontia (Theriodontia and Pariasauria) in some respects stand on an even lower structural level than the Rhynchocephalia; and, this being so, the recognition among these of Rhynchocephalian characters—originally by Seeley in *Procolophon* in 1878⁸—only the more fully justifies the belief in the primitive nature of the Rhynchocephalian

¹ Mitsukuri, K.: Journ. Sci. Coll. Tokyo, vol. iv. 91, p. 10. Cf. also Dendy, 99^c. pp. 251 & 255.

² Cf. Dendy, A., 99^c. pp. 56 & 59, and Parker, W. K., 'Challenger' Reports, Zool. vol. i. pl. 3. fig. 1.

³ Cf. Leydig, F.: 'Die in Deutschl. lebend. Arten d. Saurier,' Tübingen, 1872, p. 110; and Boulenger, G. A.: on the Ophidian *Aipysurus annulatus*, in Willey's 'Zoolog. Results,' Cambridge, 1899, p. 57.

⁴ Credner, H.: Allgem.-Verhandl. Naturwiss. Abhandlg. Berlin, Hft. xv. 1891, pp. 1-52.

⁵ Lortet, L.: Archv. Mus. Hist. Nat. Lyon, Bd. v. 1892, pp. 139. It is interesting to note that *Sauranodon* possessed procelous vertebrae.

⁶ Dollo, L.: Bull. Soc. Belge d. Géol., tome v. 1891, p. 151.

⁷ Andreæ, A.: Ber. Senckenbg. Naturf. Gesellsch. 1893, p. 21.

⁸ Seeley, H. G.: Quart. Journ. Geol. Soc. vol. xxxiv. 1878, p. 803. The pterygo-vomerine relationship is now known to be Rhynchocephalian among Anomodonts in *Procolophon* and *Galesaurus* (A. S. Woodward, 'Outlines of Vertebr. Palæont.,' Camb. 1898, pp. 148 & 152), and it is probably so in *Pariasaurus* also (cf. Seeley, Phil. Trans. vol. 183 B. 1892, p. 317). The description of a post-palatine fossa, which in all probability received a median tonsil ("bursa pharyngea") like that observed by Killian (Morph. Jahrb. Bd. xiv. 1888, pp. 659-690) for living reptiles, as the posterior nares, and of the true posterior nares (p. 317) as "anterior comma-shaped palatal vacuities," is erroneous. The study of the palatal region of this animal needs re-investigation.

Order, and of *Sphenodon*, its living representative. Since *Sphenodon* thus occupies the afore-mentioned primitive position among living reptiles—not to say among the Sauropsida as a whole—and since our classificatory systems of the Vertebrata, to be of avail, must be primarily based upon facts concerning parts capable of fossilization, the special interest attaching to the study of the development of the *Sphenodon* skeleton becomes sufficiently evident. And, as involving the Order Rhynchocephalia, the fact that in one of the most recent, and that which we have found the most rational and serviceable of classifications thereof¹, a distinction has become possible between a higher and a lower sub-order, in itself raises the interesting question whether in the development of *Sphenodon*, a member of the higher sub-order, there may not be passed through phases characteristic of the lower, to-day unrepresented.

During the thirty years afore-named no available opportunity has been lost by workers of all nationalities to study the habits and anatomy of *Sphenodon*, and a list of the resulting papers is appended to this Memoir (*infra*, p. 71). Most organs and systems have received attention. The most exhaustive contribution is that of the Japanese Osawa, which is a laborious anatomical treatise extending over 438 pp. of the Archiv für Mikroskopische Anatomie (*cf.* list, Osawa, 96–98); and, while grateful to him for this, it is with much astonishment that we have to record his final conclusion (98^b, p. 352, and 98^c) that *Sphenodon* is an Agamid—a reversion to the view of Gray (1831), adopted and afterwards forsaken by Cope², revived by Peters (70), and rejected by Günther (69, p. 624)³.

2. MATERIAL.

In 1894, when Professor Dendy was appointed to the Chair of Biology in the Canterbury College of the New Zealand University, one of us, in regular correspondence with him, sought to impress upon him the desirability of doing all in his power to secure without delay material for the study of the development of *Sphenodon*, not knowing at the time that our mutual friend, Prof. Baldwin Spencer, F.R.S., of Melbourne, had also approached him on the subject. With what enthusiasm and at what personal cost he responded to the desire, his published memoirs (Dendy, 98, 99^a, 99^b) amply testify. On hearing of his success in the field, no time was lost

¹ Boulenger, G. A.: Ann. & Mag. Nat. Hist. (6) vol. xi. 1893, p. 204.

² Cope, E. D.: *cf.* Proc. Acad. N.S. Philad. 1864, p. 227, and Proc. Americ. Assoc. vol. xix. 1870, p. 233.

³ It has always been to me inexplicable why Huxley should have refused to admit the validity of the Order Rhynchocephalia. Well do I remember how, in conversation, he once remarked to me that “*Sphenodon* is a lizard and only a lizard!” but, this notwithstanding, his final printed statement and proposal to create, for the reception of *Hyperodapedon*, *Rhynchosaurus*, and *Sphenodon*, the group of the “*Sphenodontina*” (Quart. Journ. Geol. Soc. vol. xliii. 1891, p. 691) would seem indicative of a compromise suggestive of an approaching conviction.—G. B. H.

in drawing his attention to certain of the more interesting problems (duly set forth in the pages of this Memoir) presented more especially by the skeleton and teeth of the adult animal. In reply, he expressed the hope that one of us would undertake this portion of the work, and offered, with a generosity and friendly appreciation for which we tender him our heartiest thanks, to give all the necessary material he could command if we would acquiesce. There accordingly reached us in the autumn of 1898 a large series of specimens, treated, for the younger stages with corrosive sublimate and alcohol, for the older with alcohol alone. From these, after preliminary examination, the undermentioned were selected, as embracing the period of skeletogenesis; and, concerning those which remain, Prof. Dendy has very generously acquiesced to the proposal that Dr. Elliot Smith and Mr. E. J. Bles, of Cambridge, should work out respectively the development of the brain and urinogenital organs.

List of Young Specimens Investigated (15 in all).

Stage.	No.	Date of removal from Egg.
P	87.	Jan. 25, 1898.
P*	39 a.	Unknown.
Q*†	52 a.	Jan. 30, 1899.
Q	1 a.	End of Jan. 1897.
R	142.	March 8, 1898.
R	154.	April 5, 1898.
R	159.	May 12, 1898.
R	162.	June 24, 1898.
R-S†	I.	
S†	II.	
S†	IV.	
S*	1 a.	Hatched Dec. 8-9, 1898.
S*	19 a.	„ Dec. 27, 1898.
S	138.	No details.
T†	III.	

The following are the details concerning the individuals incubated and afterwards reared in our own Laboratory.

Stage.	Length in cms.	Remarks.
R-S ^I	6.3	Died in egg, 13.11.98.
S ^{II}	7.5	{ Hatched prematurely with excessive yolk, 22.11.98.
T ^{III}	15	Hatched 14.1, died 15.99.
S ^{IV}	{ Found decomposed in egg, 14.1.99.
T ^V	15	Hatched 19.1, died 18.5.99.
T ^{VI}	17	„ 24.1, died 18.5.99.

In the foregoing list the stages and numbers are those of Dendy's series, described in the Quart. Journ. Microsc. Sci. vol. xlii. p. 10. Those marked * were found requisite as our investigation advanced, and were very kindly supplied by him at our request, and those marked † were incubated in our own Laboratory from unhatched eggs. The latter, six in number, packed close in moist sand in a 1-lb. canister with a perforated lid, were brought over by Mrs. Dendy and kept during the voyage from New Zealand in her cabin. One only decomposed, and of the five which remained, three ran the full developmental period, the enclosed young making good their own escape. These lived from three to four months, and for their reception we have added to Dendy's series a Stage T. At this stage the coloration is the same as at S, but as an advance upon that there is a complete absence of all traces of the yolk-sac and shell-breaker, and the appearance in the thoraco-lumbar region of the all characteristic median dorsal languets (spines, *auct.*), such as are already present at Stage S in the so-called "nuchal" and the caudal tracts. These appendages, whose existence is expressed in the native name Tuatara¹, are liable to no slight individual variation. Three tracts are present in the adult, viz. "nuchal," thoraco-lumbar ("dorsal"), and caudal, as recognized by Boulenger in his, the latest, diagnosis (89. p. 2), with consequent scapular and sacral intervals. Buller (76. p. 324) and Newman (77. p. 230) have called attention to the existence in the region of the cervical space of a conspicuous pigment-patch; and, concerning the numerical variation of the "spines" in the adult, they give for the "nuchal" series 10-14, for the thoraco-lumbar 15-20. From examination of eleven specimens present in our own collection and that of the British Museum of Natural History, we find the extremes range from 6 to 14 for the "nuchal" and 15 to 24 for the thoraco-lumbar series. In two specimens of our Stage T they number 10 and 18 respectively.

With a view to ascertaining the limits of individual variation, and thereby rendering the present memoir as complete as possible anatomically, we have examined all the dried skeletons within our reach—viz., the complete skeletons of nine adults, fragments of some six to eight others, and the complete skeleton of a half-grown individual in the possession of the Royal College of Science, Dublin. For the privilege of examining all but two, which are at South Kensington, we are indebted to Prof. A. C. Haddon, F.R.S., to Prof. C. Stewart, F.R.S., of the Royal College of Surgeons Museum, to Dr. R. F. Scharff, Keeper of the Natural History Department of the Science and Art Museum at Dublin, and to our friends in the British Museum of Natural History.

Beyond this, we have had recourse where necessary to dissection of six spirit-specimens in the Teaching Collection of the Royal College of Science, two of which were presented by Prof. Dendy in the spring of 1899.

¹ Cf. Newman (Taylor *cit.*), 77, p. 222.

3. METHODS AND RECONSTRUCTION.

Methods.—Dissection was resorted to only in the later stages, and wherever the elements under consideration were fully formed. Throughout the earlier stages, and in the later where necessary, microscopic sections were relied upon; and further, as for example at Stage S and in dealing with the carpus and tarsus, dissection was duly checked by section, as a means of ensuring accuracy of detail.

The microscopic sections were in all cases mounted serially, the plane of section being determined by the object in view (as set forth in the accompanying description of the Plates). After preliminary experiment with the Green Lizard (*Lacerta viridis*), it was found that differentiation of the skeletogenous tissues could best be obtained by staining in bulk with Ehrlich's hæmatoxylin, and afterwards on the slide with Grübler's orange G. For this suggestion and much subsequent aid we are indebted to Mr. M. F. Woodward, Demonstrator of Zoology, Royal College of Science, London, than whom no better manipulator or master of micro-chemical technique exists; and we found, as our work proceeded, that much time is to be saved by dissolving the orange in 70 p. c. alcohol, with the addition of a few drops of glacial acetic acid, thus eliminating the tedium arising out of the use of a mere aqueous solution. The results of this method are exceedingly satisfactory, cartilage being as a rule differentiated blue, bone in all its forms deep yellow, while the other tissues behave each in its own way.

Reconstruction.—Since the time has now arrived at which mere dissection is insufficient for the study of the facts of skeletogenesis, recourse was had to the so-called Bornean method of reconstruction from microscopic sections¹. We were under the necessity of working with thin plates, and found that if made of the Bornean mixture of beeswax and turpentine there was difficulty in preparation and liability to snap. By substituting vaseline for turpentine, we entirely overcame all this, and we can confidently recommend our mixture as reliable.

The figures which constitute Pl. III. and figs. 7 and 10 of Pl. VI. are all from models prepared from plates thus made. For the most part the sections of the animal were cut to a uniform thickness of 10 μ , and each plate made to that of 1 millim. Tracings were then drawn upon the plates, by means of the camera lucida, of sections at regular intervals, determined by the degree of magnification (every fourth section for a magnification of 25, every third for that of 33, and so on). In cutting out the tracings, trabeculæ were left where necessary for holding the parts together during reconstruction, and afterwards cut away. For the process of cutting, the best results were obtained by the use of a needle, the plates being laid upon glass.

¹ Earlier achievement in the same direction must not be overlooked. In England it stands memorably associated with the Huxleyean traditions: cf. E. T. Newton, "On a New Method of Preparing a Dissected Model of an Insect's Brain from Microscopic Sections," Journ. Quakett Microscop. Club (I.), vol. v. 1878, p. 150, and Qu. Journ. Micr. Sci. (n. s.) vol. xix. p. 340.

The tracings, as cut out, were laid flat in superposition, adhesion being effected by carefully running a heated wire along their edges. The use of colour was deemed desirable, but a possibility of error seemed likely to arise were the models coloured after completion. This, however, was obviated by colouring the tracings before they were cut out; and a perfectly reliable result was obtained by the use of ordinary oil-paint dissolved in xylol, to secure rapidity in drying. In plates thus treated, the melting together of their edges ensured the diffusion of the colour necessary to produce the final realistic result.

4. OBSERVATIONS ON THE EGG, ON HATCHING, AND ON THE HATCHED YOUNG.

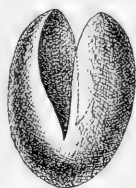
During the period of Prof. Dendy's activity, both as collector and investigator, which led to the publication of his two pioneer memoirs on the Development of *Sphenodon* (Dendy, 98^b, 98^c), there arrived in New Zealand two German naturalists—one Dr. H. Schauinsland, of the Bremen Museum, the other Prof. G. Thilenius, of Strasburg; one, if not both, of them sent out under the auspices of the Berlin Academy. Each has since published preliminary reports upon his investigations (*cf.* List, p. 74), without, however, in any way alluding to Dendy's work; and this is the more regrettable, since in matters of small detail their statements both differ from and supplement his—while it is the more unaccountable, since one of them was permitted by the New Zealand Government to explore the same island as Dendy, with the aid of the very collector he had employed. Since neither of them has written upon the skeleton, we omit further reference to their work, except so far as it concerns the newly-hatched young. Dendy, in defining his Stage S, inclined (99^a. p. 59) to the belief that the yolk is still pendant at hatching, and was unable to decide definitely upon his surmise (pp. 79–80) that the olfactory cellular-plugs which he discovered are at that period “removed.” Schauinsland, on the contrary, both figures the yolk and describes the nasal plug as absorbed shortly before hatching (98^c. p. 312), and there can be no doubt he is correct. It is but just, however, to Prof. Dendy to state that in a letter to one of us, antedating the publication of Schauinsland's notes, he had corrected his former statements (*cf.* letter to ‘Nature,’ vol. lix. p. 340), having discovered that the embryos which had led him to believe that both yolk and plug might be present on leaving the egg had been prematurely hatched.

Concerning the newly-hatched young, he further points out that the pineal eye is “plainly indicated by an irregular scale, surrounded by eight or nine others, radially arranged, and all much larger than the surrounding granules,” an observation which we can confirm. And to this we would add that the supra-pineal area of the skin of the head is at hatching transparent and pigmentless, and that it remained in that condition throughout the four months our young ones were alive.

Before passing to the main subject of this Memoir, we desire to record some observations pertinent to those communicated by us, in conjunction with Dr. Dendy,

in the above-mentioned letter to 'Nature.' Firstly as to the rupture of the egg-shell, to the symmetrical "clean cleft" character of which we drew attention. The following is a drawing of the shell of one of the eggs therein referred to which ran the full time; and in correspondence with Prof. Dendy concerning it and our suggestion that it seemed to indicate that the shell-breaker may be an actual cutting-instrument, he has authorized us to state his own view, since formed, on opening an egg at Stage S, nearly ready to hatch. He observed that the moment a small puncture is made in the shell, that "splits of itself, very suddenly and with almost explosive violence, reminding one of the bursting of a seed-vessel;" and he remarks that it has been suggested to him that the splitting may have been assisted by

Fig. 1.

Ruptured egg-shell of *Sphenodon* after the escape of the enclosed young.

Full time. Nat. size.

absorption of moisture from without, by the allantoic fluid¹. He reverts to the analogy of the well-known "Prince Rupert's drops," and concludes that "the function of the very sharp shell-breaker is probably to make the small incision;" and that when that is done, the egg, being in a condition of high tension, simply bursts open. And he is the more inclined to this view from having noted that the shell of an egg contained in sand which had been "somewhat excessively moistened" prematurely burst, and revealed within its interior a dead embryo in an insufficiently advanced stage of development.

In the afore-mentioned letter to 'Nature' we recorded certain details concerning the treatment up to the time of hatching of the eggs brought us by Mrs. Dendy. The three young *Sphenodons* which from these we successfully hatched out were kept in confinement in the incubator (Hearson's, size A I.), at the temperature at which they were hatched—viz. 25° Centigr. They were fed upon mealworms, small earthworms, cockroaches, and flies, as best obtainable. For these the individual taste was observed to vary somewhat. One little creature exhibited a decided preference for mealworms, and a "tug-of-war" for the possession of an earthworm or cockroach was a not unfrequent occurrence.

¹ Cf. also Dendy, 99^c, p. 251.

The bottom of the vivarium was covered with coarse sand to a depth of about one inch, and in one corner a water-bath was sunk; while a piece of corky-bark was introduced, which presented to the little captives a vaulted retreat. While to the latter they would readily retire, they exhibited a decided preference for the darker recesses of the chamber. Their movements during the day-time were very active, the passing of a finger-tip, the point of a pencil, or a piece of india-rubber tubing over the glass front of their dwelling, being sufficient to entice them forward. The tendency to burrow evinced itself during the second month—the actual date of the first effort being March 9th in one case observed. They exhibited a fondness for reclining in the water, in which they would lie at full length, the top of the head being usually kept above the surface. It was noticed that when, on leaving the water, the whole body was wet, an area surrounding the pineal eye always remained dry; and, concerning the use of the “bath,” it was observed that if an earthworm seized by the Lizard happened to be beset by sandy particles, recourse was had to the water and a “washing” of it before it was devoured. The prey was never swallowed as soon as seized, but always at first held between the jaws and more or less masticated.

The first ecdysis in the case of the largest specimen (TV¹, p. 5) was observed to take place about March 9th,—*i. e.* about 7 weeks after hatching.

Under the conditions above-described our little *Sphenodons* thrived and grew fat; *i. e.* they increased in length during the four months we kept them alive from 8 cm. to 15–17 cm. The near occurrence and manner of their decease, however (all three having died in the “bath” within a period of 17 days), points to a common cause of death. We suspect that this may have arisen from our having unconsciously continued to liberally feed them into the period normal to hibernation (April to middle of August¹); but, on the other hand, it may have been the mere result of over-feeding on our part (if indeed that may not have been in turn aided by the attentions of night-watchers and others who were “interested”). Whichever be the case, the salient feature of the dead animals was a superabundance of fat; and we found *post mortem* that this was evident externally in life, had we but known it, in the great enlargement and tenseness—due to its accumulation—of the dorsal languets and certain irregular folds of the skin originally described by Gray²; *i. e.* that undue distension of these may be an index of over-feeding—an observation to be borne in mind by those who may yet be so fortunate as to rear this species in captivity.

5. THE AXIAL SKELETON.

General and as to Terminology.—The adult skeleton of *Sphenodon* has been so fully described in its modern aspects by Siebenrock (93) and Osawa (98^c) that recapitulation of its general features is here unnecessary. Before, however, we proceed to details

¹ Cf. Schauinsland, 98, p. 702 (for Stephen's Island).

² Cf. Gray, 42, p. 72.

and the study of its development, we desire to deal briefly with certain facts and matters of terminology which are necessary to render clear our method of procedure. Admitting for the vertebral column of all terrestrial vertebrata a primary classification of the parts in relation to the sacrum, the time-honoured classification of the præ-sacral portion of that of the Amniota into cervical, so-called "dorsal" or thoracic, and lumbar regions, is now wholly insufficient for purposes of accurate description and comparison. The term "dorsal," being one of orientation, is misapplied. "Thoracic," although applicable to the middle region in the mammal—as embodying the region enclosed by elongated rotatable ribs and bounded posteriorly by the diaphragm—cannot with precision be applied to that of the lower Amniota, inasmuch as it presupposes the existence of a post-cardiac septum (diaphragm). The so-called "diaphragm" of birds (Huxley's "oblique septum") is præ-cardiac, and the subdivision of their cœlom into pulmonary and cardio-abdominal compartments is in marked contrast to that of mammals, which is pulmo-cardiac (or thoracic) and post-cardiac (or abdominal). Further, when it is remembered that within the reptilian series various modes of cœlomic subdivision occur, and that free ribs in both birds and reptiles may extend beyond the limits of the pulmo-cardiac region, the application of the term "thoracic" to the whole of that portion of the body which bears them is apt to lead to confusion. And when, in addition, there are considered the presence of free ribs in the lumbar region of at least the young of some mammals¹, the great variation of the ribs both in the lumbar and cervical regions of the Amniota generally, and especially that of the sternum in all its relationships, simplicity and greater uniformity in our ideas are to be ensured by enumerating the several segments of their præ-sacral vertebral skeleton by reference to the sternum—and we accordingly propose to substitute the terms *præsternal*, *sternal*, and *poststernal*, for the more familiar but arbitrary "cervical," "thoracic," and "lumbar," delimitating the regions by reference to the one organ which renders a series of terms necessary².

Vertebral Column.—Concerning the adult vertebral column as a whole, we have not met with any numerical variation of its parts beyond that involving the relationships of the sternum duly considered in the sequel. For the caudal region the maximum number of vertebrae observed by us was 34 (two less than that originally recorded by Günther [67. p. 605]), and for the præcaudal we found it always 27, viz., præsternal 8, sternal 3-4, poststernal 13-14, sacral 2, with one exception for the præsternal series. To an exceptional condition of the sacrum in another individual we shall return.

During the past fifteen to sixteen years the study of the detailed constitution and early development of the vertebral column has received an altogether exceptional amount of

¹ *Ex. Homo, juv.*: Rosenberg, *Morph. Jahrb.* Bd. i. p. 111.

² On the other hand, it has been pointed out by one of us ('Nature,' vol. lvii. p. 577) that in the Batrachia, in the absence of a costal sternum, delimitation becomes possible only in relation to the sacrum, whereupon the præ-sacral vertebrae are best dealt with collectively. The same principle applies to those Amniota in which the sternum has been lost; while in the absence of a sacrum, as in the Ophidia, the course is obvious.

attention, mainly as the result of palæontological discovery by Cope¹, Gaudry², and Fritsch³; leading to the recognition of the so-called rhachitinous, embolomorous, and other similar conditions, which have received at the hands of subsequent investigators correspondingly appropriate names. Both on the embryological and the palæontological sides, a considerable amount of evidence has been brought forward for the belief that some such complex type of vertebra as these, *i. e.* one in which each vertebral segment was made up of a series of paired elements, was the ancestral one, and that the various types of vertebral structures characteristic of the living groups may have resulted from diverse modification (inequality of growth and suppression) of these. And, in the attempt to substantiate this belief, Männer, in the latest paper⁴ on the subject, has sought to show that from the first period of its differentiation in cellular tissue, the individual "sclerotome" of the Lacertilian is a compound structure. Goette, basing his arguments, like Männer, mainly upon the study of the Reptilian backbone, has concluded⁵ that the vertebræ of the living "digitata" have arisen from the embolomorous type, and he regards the rhachitinous type as "neither primitive nor independent, but transitional." If, however, the relationships of these are really direct, we would rather transpose the order, since we regard the greater extension of the skeletogenous tissues, and consequent deeper constriction of the notochord, occurring in the embolomorous type as indicative of advance upon the rhachitinous, as already pointed out by Gadow⁶. He, working on this basis, has simplified our conceptions of the fundamental constitution of the diverse forms of vertebral structure represented among the living vertebrata, beyond his predecessors, by the introduction of a systematic terminology based on the supposition that all surviving forms of vertebræ are constituted more or less of two pairs of dorsal and two of ventral elements symmetrically disposed, and that⁷ "the solution of the composition of the vertebral column is given by the metameric repetition" of these, "the origin of which can be traced in fishes." His terms "basi-" and "inter-" "dorsalia," "basi-" and "inter-" "ventralia," are most welcome; and the arguments and conclusions drawn by him certainly furnish a possible explanation of some of the great anomalies arising out of the mere study of the adult vertebral column among living forms—as, for example, the intervertebral disposition and independence of the "chevron bones" of the Amniota, and the vertebral disposition and confluence with the vertebral bodies of the "hæmal arches" of the Urodela.

¹ Cope, E. D.: *Americ. Nat.* 1878, p. 327; *Proc. Americ. Philos. Soc.* vol. xvii. 1878, pp. 510-526; *Trans. Americ. Philos. Soc.* vol. xvi. 1886, p. 243.

² Gaudry, A.: *Enchainements d. Monde anim. Foss. Prim.*, tom. i. (Paris, 1883), p. 263.

³ Fritsch, A.: *Fauna d. Gaskohle d. Permform. Böhmens*, Bd. ii. 1889, pp. 14 & 24. *Cf.* also Baur, G.: *Biol. Centralbl.* Bd. vi. 1886, pp. 332 & 353.

⁴ Männer, H.: *Zeitschr. wiss. Zool.* Bd. lxvi. 1899, p. 43.

⁵ Goette, A.: *Zeitschr. wiss. Zool.* Bd. lxii. 1897, p. 390.

⁶ Gadow, H.: *Phil. Trans.* vol. 187 B. 1896, p. 1.

⁷ *Op. cit.* p. 50.

Certain it is that this subject, as it now stands, forms one of the most fascinating chapters in the vertebrate morphology of our time. Our own researches begin at the period of differentiation of actual skeletogenous tissue, and while, concerning the supposed original complexity and general uniformity in origin of the parts of the vertebral body, we retain an open mind, we question if, in matters of detail to be referred to in the sequel, theories, in their growth, have not been at times unconsciously read into the supposed record of facts.

First differentiation of the Skeletogenous Tissue.—The earliest stage which we have investigated is Dendy's P, and a median longitudinal section through any portion of the skeletal axis at this stage reveals the presence of a central notochord, ensheathed in a thin structureless and deeply staining cuticle or *chordal sheath* (elastica externa of Gadow [*nc.s.*, Pl. I. fig. 2]). This is seen to be in turn invested by a continuous *skeletogenous sheath*, composed of a thickly disposed mass of small cells, containing relatively large nuclei. There are some 9–10 rows of these, and their close compression gives to the tissue, when examined under a low magnifying power, the appearance of being feebly longitudinally striate. The notochord itself consists at this stage of comparatively small vacuolated cells, arranged in an irregular manner, and differentiated peripherally into the usual *chordal epithelium* (*nc.e.*). Central or other differentiation there is none.

Comparing with the foregoing a lateral longitudinal section, the superficial cell-rows of the skeletogenous layer are seen to be more closely approximated than the rest, and in addition there are (fig. 1) differentiated within the area of this more closely aggregated stratum a series of metamerically recurrent masses (*i.p.*) of cells, generally more rounded than the rest. They are the developing intercentra; wherefore it follows that in order of differentiation these are the first formed skeletal elements.

When the corresponding parts are viewed in transverse section, the skeletogenous layer is seen to completely encircle the notochord, constituting a *skeletogenous sheath*, the aggregation afore-named being apparent (*i.p.*) as a couple of symmetrical tracts which are ventro-lateral, widely separated in the trunk-region (*cf.* fig. 2), closely approximated in the ventral line in the caudal (fig. 3). The neural arches are at this stage first differentiated, in the form of bilaterally symmetrical upgrowths of the skeletogenous sheath (fig. 3, *n.a.*), separated by a wide interval in the mid-dorsal line.

Stage Q.—A transverse section through an intervertebral region at this stage shows that, concerning the skeletogenous sheath (*t.a.*, text-fig. 2 and Pl. I. fig. 6), the cells remain practically unchanged, their nuclei when examined under a high power presenting the oval contour indicative of mutual apposition, so characteristic of the earlier stage afore-described.

Comparison of a similar section through a vertebral region shows (text-fig. 3) that chondrification has there set in, but not at all points—for, while laterally hyaline cartilage is now present, in the form of paired masses (*c.v.*), continuous with the now cartilaginous neural arches (*n.a.*) and confined to the superficial layers of the

skeletogenous sheath, in both dorsal and ventral middle lines the latter (*s.s.*) has remained unchanged.

Comparison with the foregoing of a lateral longitudinal section at a slightly later stage, shows (Pl. I. figs. 7 & 8, *c.v.*) that these lateral chondrites encroach upon the skeletogenous sheath from without inwards, rapidly involving its deeper layers, until its innermost limit is reached. They also effect the replacement of the afore-mentioned median portions, but by union within the deeper layers and subsequent extension in the opposite direction—*i. e.* from within outwards, as is seen at *c.v.* in Pl. I. fig. 6, which is that of a median longitudinal section at this period.

The above described processes continue until chondrification of the vertebral portions of the skeletogenous sheath is complete, and there thus results a metameric segmentation

Fig. 2.

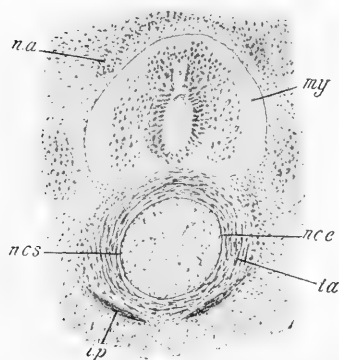
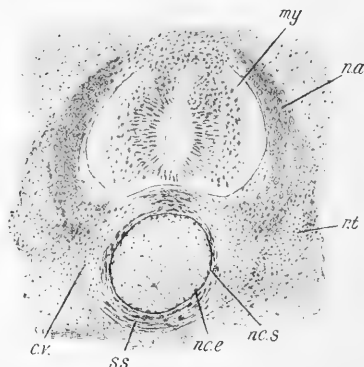


Fig. 3.



Transverse sections through the poststernal region of the trunk of *Sphenodon*. 2. Intervertebral; 3. Vertebral, drawn for comparison. Camera lucida $\times 70$.

c.v. Cartilaginous vertebra; *i.p.*, primitive paired intercentrum; *my.*, myelon; *na.*, neural arch; *nce.*, notochordal epithelium; *nc.s.*, chordal sheath; *r.t.*, trunk rib; *s.s.* skeletogenous sheath; *ta.*, inter-articular tissue (intervertebral portion of skeletogenous sheath).

of the vertebral axis, whereby a series of segments become recognizable, each comprising a centrum, an intercentrum, and a pair of neural arches; and the facts justify our regarding the centrum as of paired origin—a view which lends support to Gadov's conclusion that it represents the fused "interventralia" of the lower vertebrate forms.

As is well-known, the chevrons and præsternal or cervical intercentra present in most Lacertilia may, by shifting, come into secondary relationship either with the vertebræ in front of them¹ (by which they may even be carried down on autogenous hypapophyses, as in the neck of the Mosasaur *Tylosaurus*²), or with those behind

¹ *Ex.* Anguillæ, Varanidæ, Helodermatidæ; and, with co-ossification, Mosasaurus, some Varanidæ, and Pseudopus. (*Cf.* Boulenger, P. Z. S. 1891, p. 113, and Gadov, Phil. Trans. vol. 187 B. 1896, p. 30).

² *Cf.* Osborn, H. F.: Mem. Americ. Mus. Nat. Hist. vol. i. 1899, p. 171; and also Americ. Nat. vol. xxxiv. 1900, p. 1.

them, as in *Tupinambis*¹. This notwithstanding, since the anterior element of the whole series (that lying between the skull and first vertebra) is the first intercentrum, precision and uniformity are gained by enumerating it in correlation with the centrum behind it, and so on for the whole series which follow—as has been done, for example by Gadow, for the chevrons, though not with that uniformity which is desirable. The method mostly adopted, especially in illustrations, of associating with the numeral indicative of a given chevron that denoting the vertebra in front of it, as has been done with descriptions of the skeleton of the adult *Sphenodon* from Günther to Osawa, leads to confusion and must be given up.

Passing now to the intercentra, a marked advance is seen to have taken place in those of the anterior twelve body-segments and the tail. At Stage P the intercentral bodies are everywhere paired. At Q, fusion in the mid-ventral line has come about in the anterior region (*cf.* Pl. I. fig. 8, *i. p'*). In the case of the first four bodies, the contour of the fused product gives no indication of its paired origin, but from the fifth to about the twelfth (as determined by very careful examination of serial longitudinal sections) a median depression remains. These facts are embodied in column Q of our table on p. 27, and perusal of them would seem to indicate that fusion of the paired intercentra takes place antero-posteriorly.

At Stage P, owing to the absence of demarcation between the cranial and vertebral portions of the differentiating tissues, the enumeration of the centra had to be determined by reference to the sacral region, *i. e.* the segments had to be worked out in postero-anterior succession. The numerous practical difficulties arising from this necessity, leave us in doubt whether the first and second intercentra are or are not represented at this stage. Hence the ? in our table, column P (p. 27). This consideration would seem to throw some doubt upon the paired origin of these first two intercentra; but, judging from the fact that from segments 12 to 5 the unpaired intercentra at Stage Q still show traces of paired origin, and that in segments 4 and 3 these elements are proved to be beyond doubt originally paired, we deem it fair to conclude that the same conditions apply to segments 2 and 1.

It may be remarked that at this stage (Q) the union of the first centrum with adjacent parts is effected. While it fuses (fig. 8*a*) completely with the second intercentrum (*i. p'*), it does so only peripherally with the second centrum, and that so as to enclose at * a central mass of undifferentiated tissue.

The neural arches have at this stage completely united in the dorsal middle line and are fully chondrified.

Passing to the caudal region, the intercentra of its fourth and succeeding vertebral segments, by an astonishing rapidity of growth, have acquired a characteristic elongation, each extending downwardly into (Pl. I. fig. 7, *i. p''*) the substance of the tail, but without meeting its fellow. Although they are chondrified, and at this stage differentiated in advance of their homologues—the paired intercentra—in front, their cells

¹ *Cf.* Boulenger, G. A.: *op. cit.* p. 114.

are still more closely aggregated than those of the centra, wherefore they appear under the microscope dark and highly conspicuous.

Stage R.—This stage is most noteworthy for the completion of chondrification in the median plane (*cf.* Pl. II. fig. 11) of the vertebral bodies, throughout the whole length of the column, and for the lateral extension of these. Ossification of them has now set in, chiefly in the dorsal and ventral surfaces as seen in transverse section (Pl. II. fig. 11, *o.v.*). The neural arches begin to ossify independently of each other and the centrum, by an identical and similarly superficial process, as represented (for Stage S) at Pl. II. figs. 4–6.

At this stage a remarkable change, for which we were not prepared, is undergone by the intercentra of the segments numbering 11 to 29 (*i. e.* those between and including the third sternal and second caudal segments), *viz.*, the complete disappearance of those belonging to segments 13 to 25 (*cf.* table, column R, p. 27); and the tendency to disappearance, to an extent which renders it difficult to identify their presence, for segments 11 and 12 and 26 to 29. We are unable to say at this stage by what process this removal is effected, whether by absorption into the intervertebral tissues or otherwise; but, in view of the discovery of this remarkable fact, it is the more astonishing to note that while one pair (*viz.* those of the third caudal segment) remain in their primitive condition, those which follow this in order of succession behind, while still unossified, have coalesced distally, enclosing the caudal canal, to form the so-called “chevrons,”—which are thus proved to be the direct derivatives of primary paired intercentra.

Stage S.—Viewed in median longitudinal section, the salient advances at this period are seen to be four in number. Firstly, the ossific tracts, described in the previous stage (Pl. I. fig. 10, *o.v.*), when viewed in transverse section (Pl. II. figs. 4 & 5), are seen to be extending into the lateral cartilaginous expansions, which are being rapidly absorbed over the areas marked †. Internally to these ossific centres and immediately surrounding the notochord, there are marked signs of calcification revealed by the selective action of our reagent. Exactly the same processes take place in the ossification of the centrum of the atlas (*os odontoideum*) as of an ordinary vertebra (*cf.* Pl. I. fig. 9 *a'*).

The advance in ossification of the vertebral bodies (*o.v.*, Pl. I. fig. 10) is seen to go on hand in hand with the assumption of a more truly hyaline character by those portions which are still cartilaginous. These (as viewed in longitudinal section) are seen at the same time to undergo a marked change in shape, becoming thinned over the centre of bony deposition and thickened at and towards their extremities—*i. e.*, an inverse development of bone and cartilage is recognizable, in proportion as the centre of each developing vertebra is approached.

In the intervertebral regions (*t.a.*, Pl. I. fig. 10) the cells of the skeletogenous sheath, still closely crowded, retain, in the elongation of their nuclei, a character originally

common to the whole sheath; but there has appeared around them a feebly hyaline matrix. The now clearly recognizable differences in the parts generally admit of the application of the term *interarticular tissue* to these intervertebral areas; and we desire to emphasize the fact that though they are feebly hyaline, "intervertebral disks" are not present—the hyaline matrix, dense and resistant for the vertebral bodies, diminishes markedly as the extremities of the centra are reached, and at these fades into the more flexible interarticular tissue, there being no hard and sharp line between the two.

The process of differentiation at this stage is most noteworthy for the full formation of an important constituent of the individual vertebra, which it so happens our reagents differentiate with startling effect. This, which we propose to term the *chordal plate*, is located transversely in the central and most constricted part of the developing vertebra. We have encountered it (Pl. I. fig. 10, *n.p.*) in all regions of the column, from the first (odontoid) vertebra (fig. 9) to well into the region of the tail. Microchemically, it reacts in a totally different manner to the reagents we have employed to anything else thus far described, wherefore there is no room for ambiguity concerning it. Its general matrix, which is extensive, stains a deeper blue than any other form of skeletogenous tissue which is present, and when examined under a high power its very conspicuous appearance is found to be due to the extent of its matrix and the presence of regular circular spaces, each filled by a cell which hardly stains at all and contains a conspicuous rounded nucleus. From its general appearance and disposition we have no doubt that it represents the so-called *chordal cartilage* described by Gegenbaur in 1862¹ in the Urodela and Reptilia, and since observed by Field, Fraser, and Stöhr in certain allied forms and by Goette in the Anura.

Gadow has given (*op. cit.*) an admirable summary of the work of these investigators, all of whom regard this as chordal in origin, and of others who seek to disprove that. With the latter he is himself agreed. He deals with the question in full in Lacerta and the Geckos among Lacertilia, and since we are dealing with Sphenodon, it is with his statements that we are alone concerned in detail. Having referred (*op. cit.* p. 11) to an "occasional perforation of the elastica externa" in the Urodela, he is most emphatic as to the rending asunder and destruction of the chorda (p. 26) during the formation of the plate in certain Lacertilia. He describes this plate as a septum of which the cells "retain the appearance of young or embryonic cartilage." Dealing with the embryonic Lacerta, he asserts (p. 24) that he is "absolutely certain this so-called chordal cartilage . . . does not exist, if thereby be understood cartilage which is produced by the conversion of chorda cells; nor does this cartilage invade the chorda." His context shows this statement to be based mainly upon the examination of transverse sections, of which he says that they "allow the elastica externa to be traced as a continuous, unbroken line, which becomes irregularly folded, or creased, as

¹ Gegenbaur, C.: Untersuchg. z. vergleichd. Anat. d. Wirbelsäule b. Amphib. und Rept. 4to. Leipzig. 1862.

the sections approach the septum"; and he adds that "the cartilage of the latter is nowhere in direct contact with the cells of the chorda." The figures which illustrate his memoir are unfortunately diagrammatic, but that of a longitudinal section of the caudal vertebra of an adult *Haplodactylus* (p. 26), taken conjointly with the descriptive text and the associated remark that "in *Phyllodactylus* the chorda is only constricted," leaves little doubt in our minds that he would regard the chordal plate as ectochordal. We, on the other hand, are as emphatic to the contrary as concerning *Sphenodon*¹, since we are convinced that in that animal it is endochordal and intimately associated with the chordal epithelium in origin, as asserted by Gegenbaur.

It first appears at Stage R (Pl. II. fig. 11, *n.p.*) at the periphery of the chorda, and entirely within the chordal sheath, which by our method of treatment stains at all points light yellow as opposed to the blue of the chordal plate. On comparison of Stage S with R (fig. 11), it will be seen (Pl. II. fig. 12) that the plate increases by a process of inward proliferation. When at S it is worked out in detail in longitudinal section, two important facts are very evident, which are wholly irreconcilable with the theory of an ectochordal origin—viz., in the first place, that the tissue of which the plate is peripherally composed can be traced into continuity with the chordal epithelium, in a manner which suggests that it arises from this by special activity of its cells; and, in the second place, that its antero-posterior faces show no sharp line of demarcation from the substance of the notochord, but rather, on the contrary, a passage into it—the faces of the plate being irregular, and, as it were, sending prolongations of the matrix into the chorda (*cf.* Pl. I. fig. 10). The matrix of the plate is often seen to be feebly differentiated as its centre is reached, and in median longitudinal section a gradual transition into the central cells of the chorda may be observed².

Interesting, in consideration of recent discovery concerning the truncal origin of the amniote occiput, is the fact that at this stage there is present, wholly within the central tissues of the chorda (as it were in very testimony to the origin from this of the plate-tissue), a similar differentiation; and the fact that the distance between it and the chordal plate of the os odontoideum is about equal (*cf.* Pl. I. fig. 9, *n.p.*) to that between the latter and the plate next in order of succession behind, is not without significance. Going back to Stage R, we find this intrachordal mass represented by an essentially similar, though somewhat irregular, differentiation of the chordal epithelium, over the whole length of the intracranial notochord (Pl. I. fig. 9), with

¹ *Cf.* our footnote and reference to Zykoff, on p. 22.

² Dr. Gadov has courteously allowed us to compare his sections with our own. We can confirm his discovery of the ectochordal origin of the plates in *Lacerta*. His sections of *Gecko*, however, are in complete agreement with ours of *Sphenodon*. We conclude that the plates may arise in two independent ways; and we would accordingly distinguish between the Lacertan type in which they arise by inward extension of the skeletogenous tissues with accompanying constriction of the cuticular sheath (elastica) and the *Gecko-Sphenodon* type, in which they are chordal and lie at all stages within this. A most interesting result, but by no means without parallel in the animal kingdom.

accompanying indications of there having been a similar change in the general substance of the chorda and the adjacent tip of the odontoid vertebra.

The neural arches at this stage call for no special comment. Turning to the intercentra, a further suppression of the primary paired series has to be recorded—viz., that of the bodies related to segments 10 to 12 and 26 to 29, thus giving a condition of the complete absence of these between and including 10 to 29. With careful focussing the disappearing primary intercentra (the mode of removal of which we were unable earlier to determine) can be at this stage observed to lie wholly within the substance of the skeletogenous tissue (cf. *i.p.*', Pl. I. figs. 9 & 10); and by comparison of the several segments we have convinced ourselves that their disappearance is not due to a process of absorption and decay, but to one which may best be described as a sharing in the progressive differentiation of the skeletogenous tissues—i. e., there is no loss of substance, but merely a histological change, leading to a loss of individuality.

On the completion of this remarkable process, the intercentra are present only for the segments 1 to 9 and from the 30th backwards, i. e., in precisely those regions in which in the Lacertilia they are most generally retained; and, as concerning the more precise limitations of this intercentrumless area, this comparison becomes more close as the development of *Sphenodon* advances—until a passing condition is reached in which, as regards its intercentra, the backbone becomes, as it were, that of a Lacertilian. The anterior intercentra remain unossified, but it is during this stage that the caudal ones (chevrons) ossify, and that as the result of a superficial deposit, which in its early condition, as is the case with the neural arches, forms a bony shell (cf. Pl. II. fig. 13, *i.p.*", and figs. 4 & 5, *na.*). Owing to the rapidity with which this process is effected, we have not been able to ascertain whether ossification arises at more than a single centre.

Stage T.—The most conspicuous feature of this, the first stage after hatching, is the great extension of ossification and calcification, with accompanying constriction of the mid-vertebral areas and a general dawning of the adult characters. The process of ossification in the centra (*ov.*, Pl. I. fig. 13) has invaded all but the innermost two to three rows of cells, which are still but calcified; and it is densest at the point of greatest constriction. Both within the intervertebral areas (*t.a.*) and the central substance of the chordal plates (*u.p.*) calcification has become highly conspicuous, and in the case of the latter it extends into the processes afore-mentioned, which pass into the chorda-tissue.

The cells of the skeletogenous tissue which mark the boundary-lines between the intervertebral masses and the vertebræ have undergone a complicated rearrangement. These lines are delimitable by the fact that the nuclei of their cells, which are small, are vertically disposed in close aggregation, as compared with those of the central intervertebral series which are larger and run parallel to the longitudinal axis. Those

of the ends of the vertebræ, which during the earlier stages were structurally uniform with the cells adjacent, have at this stage become large and rounded, whereby their matrix is less conspicuous. Once again there are no structures recognizable which merit the term "intervertebral disks," nor is there any discontinuity of parts.

At this stage a still further numerical reduction of the primary intercentra goes on, their disappearance involving segments 5 to 9 and segment 30 (*cf.* table, column T, p. 27), leaving only four present in the præsacral region and traces of a fifth. The third, and probably the second and first, at the same time commence to ossify, which they do endogenously. For certain of the segments which have lost all traces of their primary intercentra, there now takes place the formation of an entirely new set of parts, remarkable no less for their time of appearance than for their detailed structure. These, which arise in relation to segments 9 to 13, appear wholly beneath, though in close apposition medially with, the interarticular masses (*t.a.*, Pl. I. figs. 13, 14), but with them they have at first no sort of connection. Laterally quite free of them, they lie between them and a tract of coarse fibrous tissue which (*f.t.*) besets the ventral face of the vertebral column. Each of these *secondary intercentra* stains deep yellow, as does ordinary bone. The most remarkable character of them, however, is the presence of a very dark and deeply-staining central portion (*cf.* fig. 14), which is highly conspicuous under a high power of the microscope, and into which there pass convergently coarse fibres arising from the underlying tissue, which by their refractability are easy of observation and impart to the bodies a highly distinctive character. These secondary intercentra are from the first median and transverse, and in this they differ *in toto* from the primary, which arise in pairs.

Adult Vertebral Axis.—On the anatomy of this we have nothing that is general to add. Developmentally, the most noteworthy advances, apart from the mere completion of the vertebral bodies, notochordal plates, and chorda, concern the interarticular tracts (which have become more distinctly fibrous) and the intercentra (which now are finally present along the whole length of the vertebral column). The tail-vertebræ and their special peculiarities will be considered later.

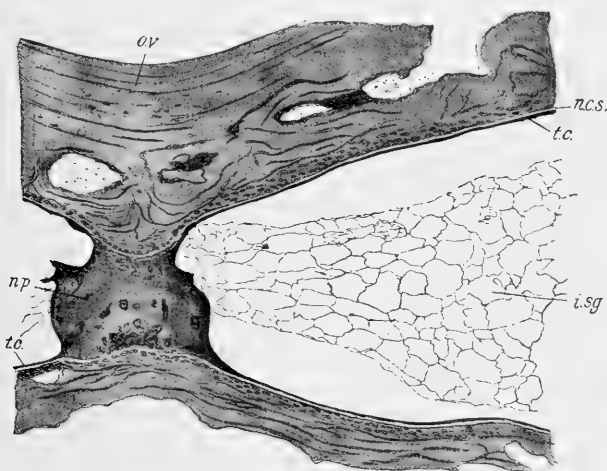
Goette has recently briefly described¹ the detailed structure of the fully-formed vertebra of *Sphenodon*, but that imperfectly, and judging by his figures from apparently none too well-preserved material. He omits mention of the chordal plate, and describes the chorda remnant as passing continuously through the vertebræ. He further remarks upon the peculiar constitution of the osseous tissue of the vertebra, which he regards as "no true bone," but rather to be compared in part to a poorly-celled calcified cartilage, with enclosed medullary nests, and of an exceptional type for the living Amniota.

We figure longitudinal sections from the sternal region of the adult backbone, stained with hæmatoxylin (Pl. I. fig. 15). The intervertebral tissues are now strongly

¹ Goette, A.: Zeitschr. wiss. Zool. Bd. lxii. 1897, p. 364.

fibrous, and on the ventral side they, together with the subvertebral fibrous tissue (*f.t.*), have attained to full differentiation. Their cells are arranged in parallel series, with an accompanying loss of individuality, the tissues having the appearance of being permeated by widely-separated parallel rows of small and elongated nuclei. While peripherally this parallel arrangement becomes more conspicuous, in the deeper layers the fibres become stronger, their attachments to the bony vertebræ appearing more marked, as the result of their greater avidity for the stain. Owing to the increase in thickness of the bony shell of the vertebral body (still largely composed throughout its inner moiety of calcified cartilage), the chordal plates (Pl. I. fig. 15 and text-fig. 4, *n.p.*) are comparatively insignificant as compared with the earlier stages. They are, however, present, and, owing to their completely septate nature, the chorda is now broken up into a series of elongated and recurrent interseptal segments, each of which is seen to be bounded not by the chordal epithelium hitherto recognizable, but by a deeply-staining and structureless cuticle, which passes into the faces of the plates, the superficial portions of which stain correspondingly with it.

Fig. 4.



Median longitudinal section of the adult vertebral column (caudal region) of *Sphenodon*, to show the tunica chordæ (*t.c.*) and its relationships to the chordal sheath and plate. Camera lucida, $\times 70$.

isg., interseptal segment of chorda; *ncs.*, chordal sheath; *np.*, chordal plate; *ov.*, osseous vertebra; *t.c.* tunica chordæ.

This cuticle, which we propose to term the *tunica chordæ* (text-fig. 4, *t.c.*), would appear to represent the chordal epithelium; but that it underlies and is independent of the chordal sheath (*ncs.*) is proved by the fact that this stains lightly and can

therefore be easily traced and seen to be continuous along the whole length of the vertebral column. We have searched in vain for evidence of the "occasional breaking-down" of the cuticular sheath (el. interna) in the vertebral regions as supposed by Zykoff for Siredon (Bull. Soc. Nat. Moscou, Bd. vii. 1893, p. 34).

The main cells of the chorda do not undergo any marked change, but in the centre of each interseptal mass, at the point coincident with that of greatest flexibility, there has now arisen, apparently by accumulation of a fluid contents, a conspicuous globular vesicle (Pl. I. fig. 15, *v.c.*), which we propose to term the *vesicula centralis*, and assume to be in some way associated with facilitating the movements of the parts.

Goette, by an ingenious argument, has drawn the conclusion (*op. cit.* p. 366), primarily from the study of the caudal region, that in Sphenodon the vertebrae are not truly amphicœlous. He extends this conclusion with qualification to the trunk-vertebrae, which he figures as transmitting an uninterrupted notochord. Osawa has adopted his view and applied it to the vertebral column generally (98^a. p. 104). We defer consideration of the caudal region, which is specialized on its own lines, till later, but acceptance of Goette's view nevertheless depends entirely upon what we are to understand by an amphicœlous vertebra. As constituted in many bony fishes, this type of vertebra, at first sight solid, at its central and most completely constricted region, is in reality perforated by a minute aperture or *canalis dicentralis*, for transmission of a delicate thread-like process of the notochord connecting the adjacent inter-vertebral masses. If such be termed an amphicœlous vertebra, as is customary, the mere continuity of this notochord in Sphenodon would be no justification for disregarding the accustomed terminology under which its vertebrae are described as amphicœlous. If, on the other hand, by an amphicœlous vertebra be meant one centrally solid and with excavated extremities,—*i. e.*, a vertebra of which one or both articular faces have not become condylar or flattened—then the term may be applied to Sphenodon, the peculiar characters of its vertebrae being in this case the great depth of its concavities. Inasmuch as we have shown the chordal plates to be notochordal derivatives, we agree with Goette, in a sense, as to the presence of a continuous notochord, which on the whole simplifies the customary conception of the Rhynchocephalian vertebra. If, however, for argument's sake we dismiss the chordal plate with the rest of the chorda, the characters of the Sphenodon-vertebra become more nearly comparable to those of the cylindroidal type to which Credner has specially drawn attention in Palæohatteria (*op. cit.* p. 492), which may or may not have been plate-bearing. Viewed from this standpoint, the extension of Goette's argument by Osawa, instead of supporting his defence of the supposed Agamid affinities of Sphenodon, weakens it to an unexpected degree.

Passing now to the caudal region, the most important facts concerning the

vertebral axis (apart from outstanding processes and chevrons) lie in the study of the "splitting" phenomenon and the intervertebral chorda. Since the days of Cuvier, a good deal of interest has centred in the study of this process, by which the Lacertilian tail may be cast off. Hyrtl, Gegenbaur, Müller¹, and Leydig have more especially studied its details, which involve to a conspicuous degree the chordal plate, as Gegenbaur first pointed out. Gadow has recently summarized our knowledge of the nature and extent of the subdivision-line recognizable on the exterior of the vertebra capable of "splitting" among certain Lizards; and perusal of his statements will show that as to its position and relationships to the neural arch and transverse processes variability may be recognized, the "split" subdividing the vertebra in some cases into equal, in others into unequal portions. In *Sphenodon* this suture usually first appears on the caudal vertebræ numbering 6 to 8, and it may be present for all posterior to it. Günther, who first described it in *Sphenodon*, states (67. p. 606) that it "passes through the middle and behind the transverse process." Gadow, on the other hand, figures it as passing in front and subdividing the vertebra into approximately equal halves, of which the posterior bears both transverse processes and neural spine. With this we are in agreement (*cf.* Pl. I. fig. 18), but we have noted that while the suture may occasionally pass through the expanded base of the transverse process², it may also subdivide the neural spine (as in Pl. I. fig. 20) in a manner anticipatory of the more symmetrical division which, according to Gadow (p. 29, figs. 22 and 23), appears to involve the anterior neural spine³ of *Lacerta ocellata*. And further, the characters of the first three suture-bearing vertebræ prove conclusively that although an elongation is effected when the suture is present, it is a subdivision and not a duplication which has taken place, since in vertebræ which are in all other respects identical with those immediately in front, the suture, which is restricted to the centrum in nos. 9 and 10, passes gradually up to the arch, assuming the condition characteristic of those behind.

We have noted that in the adult vertebral column both halves of the splitting vertebra send down minute but definite autogenous hypophyses, which have not before been described. These (*ha'*, Pl. I. fig. 18), when examined *in situ*, are found (fig. 19) to extend into the walls of the hæmal canal, to which they act as extra supports.

¹ Müller, H.: Ueber Regeneration d. Wirbelsäule u. d. Rückenmarks b. Triton u. Eidechsen. 4to. Frankfurt, 1864. For other references, see Gadow, *op. cit.*

² We consider Cligny in error in his recent argument ("Miscell. Biologiques," Travaux d. l. Station Zool. d. Wimereux, tom. vii. 1899, p. 432), that the power of fracture and the "double pleurapophysis" are associated with ancestral characters. The probability that the centra of the Amniota are compounded of the "intra-ventralia" alone is completely opposed to it.

³ So called by Cope in *Dipsosaurus* and *Sauromalus*, Proc. Amer. Phil. Soc. vol. xxx. 1892, pp. 202-205. Comparison with *Sphenodon* renders it extremely doubtful if this is a product of division, as assumed by Boulenger (P. Z. S. 1891, p. 169). We would rather regard it as a secondarily formed outgrowth like the autogenous hypapophyses which we herein describe.

Equally significant, as proving that the splitting phenomenon is secondary, is the fact, already pointed out by Gegenbaur in 1864, that the changes which render it possible appear as, by ossification, the vertebra is assuming the adult condition; and in support of this we are able to state that the bony centrum and chordal plate (both of which become split as the adult condition is realized) are in the developmental stages complete. The first appearance of subdivision is at Stage T. In fortunate sections of the adult we have been able to determine the probable method of splitting, and that it is, at least to a large extent, due to invasion of the bony vertebra and ultimately of the chordal plate itself (cf. *np.*, Pl. I. fig. 17) by the surrounding tissues, with accompanying absorption, since in sections in which the process was going on we find an inward extension of these tissues into the parts already ossified, with an accompanying peri-vertebral striation radiating from the split (cf. Pl. I. fig. 17, *x.*) such as we have encountered nowhere else. The bony vertebræ, however, continue to thicken after the first appearance of the split, and nowhere more so than at its opposite edges; wherefore it follows that by this, which is a growth process, the split is extended outwards.

We find in the intervertebral regions of the tail that a series of changes of a somewhat remarkable and intensely interesting order are undergone. Goette has recently described them in part. He calls attention (*op. cit.* p. 365) to the fact that in the caudal region the opposite ends of the vertebræ, which in the trunk are usually directed outwards, are inwardly thickened, and that they so constrict the vertebral canal that it is most spacious within the vertebra and narrowest at its extremities. In this respect the caudal vertebra presents a striking contrast with that of the trunk-region, in which the ends are widely open and the centre is contracted. He asserts that correlatively with this constriction an ingrowth of the intervertebral mass, already foreshadowed in the trunk-region, has effected a complete blocking of the intervertebral area, with accompanying segmentation of the chorda. When first examined, the intervertebral regions of the tail of a mature *Sphenodon* do appear to be compact, as Goette asserts; but when further investigated in well-preserved material the parts there present are seen to be complex, and to bear to one another a relationship essentially similar to that which the chordal plate bears intracentrally to the vertebral body. The interseptal chordal segment (Pl. I. fig. 17, *i.sg.*) becomes divided throughout its intervertebral region by a cartilaginous plate (*u.p.*) lying wholly within the chordal sheath, continuous with the tunica chordæ, and having essentially the same structure and evidently the same origin as the chordal plate (*u.p.*). Indeed, the first indications of this are met with at Stage T, as a well-marked thickening of the tunica chordæ and its associated cellular tissue. As fully differentiated, this, which we propose to term the *intervertebral chordal plate*, in contradistinction to the chordal plate which is *intravertebral*, reveals terminal calcifications, and a centrally less dense area at the point where movement of the parts is greatest, which, while providing for the necessary flexibility, furnishes additional support. It would thus appear that under the weakening influence associated with the

splitting of the strongest part of the vertebral complex, a compensating development is deliberately initiated in the intervertebral—a process to which the term of Dohrn and Kleinenberg, “substitution of organs,” may be not inappropriately applied; and beyond the extent to which these intervertebral plates may furnish support and be concerned in determining points of muscular attachment, we are inclined to regard the intravertebral plates as direct agents in the formation of the axis of the reproduced tail. This matter, however, requires further investigation. There remain only for consideration the definitive intercentra of the region of disappearance of those of the primary series, viz. segments 5(?)–6 to 30. The intervertebral region of each of these shows an intercentrum of considerable proportions (Pl. I. fig. 15, *i.s.*). This, the *secondary intercentrum*, agrees with those already described (*antea*, p. 20) in lying outside the skeletogenous tissues, as figured by Goette (*op. cit.* pl. xvii. fig. 25, *x*). Not wholly so, however! The most distinctive character of these remarkable bodies is a sharp demarcation into a greater feebly-staining outer portion and a lesser inner one, which differentiates darkly and, when viewed in section, tapers into the intervertebral mass. The cells of their inner moiety are more numerous and much larger than those of their outer; and since in the mode of disposition these are linear with those of the intervertebral mass, they would appear to be derived from it. If this be so, these definitive secondary intercentra would appear to represent those to which we originally applied the term, but with a superaddition of parts derived from the intervertebral tissues. Be this as it may, their formation finally completes the series of intercentra, which are now present throughout the whole length of the column.

Typically these secondary intercentra arise singly, as median and transverse masses. In one case, however (*i.s.*, Pl. I. fig. 16), we have noted that for segments 12, 13, and 16 to 20 (7 in all) they are paired. Boulenger has drawn attention (P. Z. S. 1891, p. 170) to the existence in *Lacerta ocellata* of paired intercentra in the posterior sacral and anterior caudal regions, and Leydig has figured a similarly-paired condition of one of the præsternal intercentra of *L. agilis* (*op. cit.* pl. iv. fig. 53). In the absence of any knowledge of secondary intercentra in the Lacertilia, we conclude that while in both species the paired elements are of primary order, in our exceptional *Sphenodon* those of the post-sternal region, which are paired, would seem to be of secondary, and that these may therefore be variable as to their median or paired nature.

Comparison of the caudal region of *Sphenodon* with that of *Lacerta ocellata* as described by Boulenger would seem to justify the conclusion that in the chevrons primary intercentra are alone represented. We find, however, that in the case of the first 4–5 this is not wholly so. In the adult *Sphenodon*, these are characterized by the fact that their proximal ends are united, as pointed out by Dollo in 1883¹, whereby they appear to overarch the caudal canal. Credner has confirmed this observation, and

¹ Dollo: Bull. Mus. Hist. Nat. Belg. tom. ii. 1883, p. 324.

with equal acumen has made it the basis (*op. cit.* p. 501) of determination of the isolated chevrons of Palæohatteria as median caudal.

Seeking the explanation of this overarching in Sphenodon, it occurred to us, having proved the chevrons proper to be permanent primary intercentra, that their united "proximal ends," being serial with our secondary intercentra, may be the homologues of those and that the anterior 4-5 chevrons are therefore complex ¹. In support of this conclusion we would point out that at those stages at which the secondary intercentra are undeveloped (Pl. I. fig. 12 and Pl. II. fig. 13) the extremities of the chevrons in question are in no way united; and proof of its accuracy has come to us in a specimen belonging to the Dublin Museum, in which (Pl. I. fig. 21) the right half of the anterior chevron (*i.p.*) and the overarching lobe (our secondary intercentrum) have remained distinct.

We append, in tabular form (p. 27), a synopsis of the complicated series of changes undergone by the successively formed sets of intercentra; and in conclusion desire once again to emphasize the fact that in the most fully differentiated state the bony vertebra and the fibro-cartilaginous interarticular masses of Sphenodon are organically continuous.

We are constrained to do this as Cope more particularly ², and Gadow, though with greater caution ³ (reading as we believe theory and expectation into fact), have referred to the intervertebral masses in terms applicable only to discontinuous skeletal parts.

The so-called "Pro-atlas."—The most recent view expressed as to the morphology of these debateable elements is that of Gadow, who (*op. cit.* pp. 12, 13, and 37) has come to regard them as parts of the atlas—the serial homologues of his "supradorsalia" of the supposed ancestrally composite vertebra. In the conclusion that the atlas was thus originally more complex than has hitherto been supposed, and that the atlas and "pro-atlas" represent one vertebra, he has been followed by Osborn (*op. cit.* p. 173), who, from the study of the palæontology of the Reptilia, has come to regard the atlas as composed of five pieces and "persistently rachitomous." Despite all attempts to discover facts which might help further to elucidate this question, we have failed. Appeal to the nerves availed us nothing, and all that we can add is that the "pro-atlas" so-called is præformed in paired cartilages (Pl. II. fig. 3, *p.a.*), which at Stage Q arise independently of both the cranium and the rest of the vertebral column, and are imbedded in the tendons of the dorsal skeletal muscles, near the point of attachment of these to the exoccipital, and that their articulation upon the skull is secondarily acquired (*cf.* Howes, 90, p. 357).

¹ We fully concur in Boulenger's refutation (Ann. & Mag. Nat. Hist. ser. 6, vol. xii. 1893, p. 60) of Dollo's hypothesis that "hæmapophyses are homologous in all Vertebrata."

² Cope, E. D.: Trans. Americ. Philos. Soc. vol. xvi. 1886, p. 248.

³ Gadow, H.: Phil. Trans. vol. 187 B. (1896), pp. 33 & 51. The term "intervertebral disks" is apt to create the impression of existence of independent elements.

		P.	Q.	R.	S.	T.	Adult.
Cervical.	1.	?	U.	U.	U.	U.	U.
	2.	?	U.	U.	U.	U.	U.
	3.	P.	U.	U.	U.	U.	U.
	4.	P.	U.	U.	U.	U.	U.
	5.	P.	U.†	U.	U.	?	?
	6.	P.	U.†	U.	U.	—	F.
	7.	P.	U.†	U.	U.	—	F.
	8.	P.	U.↓	U.	U.	—	F.
Trunk.	9.	P.	U.	U.	U.	F.	F.
	10.	P.	U.	U.	—	F.	F.
	11.	P.	U.	?	—	F.	F.
	12.	P.	U.	?	—	F.	F.
	13.	P.	U.	—	—	F.	F.
	14.	P.	P.	—	—	—	F.
	15.	P.	P.	—	—	—	F.
	16.	P.	P.	—	—	—	F.
	17.	P.	P.	—	—	—	F.
	18.	P.	P.	—	—	—	F.
	19.	P.	P.	—	—	—	F.
	20.	P.	P.	—	—	—	F.
	21.	P.	P.	—	—	—	F.
	22.	P.	P.	—	—	—	F.
	23.	P.	P.	—	—	—	F.
	24.	P.	P.	—	—	—	F.
	25.	P.	P.	—	—	—	F.
Sac.	26.	P.	P.	?	—	—	F.
	27.	P.	P.	?	—	—	F.
Caudal.	28.	P.	P.	?	—	—	F.
	29.	P.	P.	?	—	—	F.
	30.	P.	P.	P.	P.	—	F.
	31.	P.	P.	Chev.	Chev.	Chev.	Chev.—F.
	32.	P.	P.	Chev.	Chev.	Chev.	Chev.—F.
	33.	P.	P.	Chev.	Chev.	Chev.	Chev.—F.
	34.	P.	P.	Chev.	Chev.	Chev.	Chev.—F.
	35.	P.	P.	Chev.	Chev.	Chev.	Chev.
		↓	↓	↓	↓	↓	↓

Fig. 5.—Tabular statement of the order of arrangement and succession of intercentra for Stages P to T and the adult.

P. Primary paired intercentra. U. Unpaired intercentra of primary order. — Intercentra absent.

F. Secondary intercentra. Chev. Chevrons. † Medially constricted.

Ribs and Sternum.—Ribs were attributed by Günther to the segments between and including the fourth præsternal (cervical) and the second sacral. Discriminating between the osseous rib as a “pleuropophysis” and its unossified ventral portion as a “hæmapophysis,” he further distinguished between those vertebræ in which the latter is fully developed as “dorsal” and those in which it is reduced as “cervical” and “lumbar” respectively.

For the caudal region he describes the presence of “transverse processes” and

rightly records a transverse disposition of the first and second and the forwardly-directed one of those which follow (*loc. cit.* p. 606). In attributing the first cervical rib to the fourth vertebra he was in agreement with Owen, who first discovered this¹. Baur, however, later described in an individual specimen the presence of a free rib upon the third vertebra, and showed at the same time that (86°, p. 736) the so-called caudal "transverse processes" of the adult represent co-ossified ribs. Osawa (98°, p. 485) declares his inability to confirm the presence of the latter; but, with Gadow, we can do so, and can confirm the occasional presence of a rib to the third præsternal vertebra. Neither Gadow nor Baur state the number of caudal ribs observed. Our own investigation shows them to be present (Pl. I. fig. 12) for at least the eight anterior caudal vertebrae. Posteriorly to these, according to Günther, the "transverse processes" become rudimentary, and we have no material to prove whether they do or do not ossify separately. The osseous rib-formula may accordingly now be rendered as follows, allowing for the possible presence of additional caudal ribs yet to be discovered:—

Præsternal	5-6
Sternal	3-4
Poststernal	13-14
Sacral	2 with variation.
Caudal	8 observed at Stage S.
<hr/>	
Average	33

In the adult animal the anterior præsternal ribs alone stand related to both intervertebral and vertebral bodies (*cf.* Pl. II. figs. 1 & 2), the rest either articulating or, as in the case of the caudal and apparently in individual cases of the last three poststernal, becoming co-ossified with the vertebrae alone. Baur, in describing the præsternal ribs, has drawn attention to the existence of supposed ligamentous homologues in relation to the first and second vertebral segments, and to the third where an osseous rib is absent. Of these ligaments, he describes the first as single-headed and attached to the first intercentrum, the second and third as double-headed and attached to both intercentrum and transverse process of their corresponding vertebrae (*i. e.* those behind), and he points out that in its attachment to the intervertebral body the lower ligamentous tract agrees with the capitulum of the rib borne upon the fourth vertebra, which he, with Owen and Günther, describes as two-headed. Of the fifth rib, he rightly points out that it is the capitulum which is reduced, wherefore it follows that if his identification of these ligamentous tracts as vestigial ribs is correct, the first and fifth are diversely modified.

We can confirm (*cf.* Pl. II. fig. 2) the general accuracy of his description and

¹ Owen, R.: *Cat. Osteol. Series R. Coll. Surgeons Mus.* vol. i. 1853, p. 142.

can extend his discovery of an osseous rib for the third vertebra to an individual of Dendy's Stage S (Pl. II. fig. 1) and to adult specimens in the R. College of Surgeons and British Museum. If his "ligamentous ribs" are really such, it is reasonable to suspect that at some developmental stage they may be either definitely skeletogenous or may show traces of their supposed skeletal origin. After careful search, we are only able in support of this conclusion to point to the existence within the third ligament of an individual of Stage S of an insignificant cartilaginous nodule. The fact that no trace of a corresponding nodule was forthcoming in the two specimens of Stage R examined, leads us to regard the afore-mentioned case as an individual one of the presence of a vestigial rib.

Concerning the relationships of these supposed ligamentous ribs, there is a detail not recorded by Baur. As viewed at first sight (fig. 2), the double attachment would seem suggestive of a two-headed rib; but, in the case of the most distinctly two-headed osseous rib (*viz.*, that of the fourth præsternal segment), the osseous capitulum and the supposed ligamentous one coexist, while for both this rib and those behind it, in which the capitulum is unrepresented in bone, the supposed ligamentous portion of the rib, instead of passing into the substance of the osseous one, as should be the case were it a constituent of the rib, merely skirts the lower border of that with an accompanying attachment of its fibres. Throughout the region of insertion anteriorly of the muscles termed by Osawa "costo-cervical," it leaves the rib and passes on as an independent structure, in the manner delineated in Pl. II. fig. 2, *m.*—in exactly the manner which would result from an intimacy of mechanical relationship. When to this is added the disproportionate development of the first of the so-called "ligamentous ribs," which is in reality for the most part a muscular mass, we doubt how far these structures really represent ribs wholly or in part, and confess ourselves unable to definitely decide the question either way¹.

Turning now to the rest of the præsacral ribs, as concerning their heads and articulations alone, we find as we pass back from the fifth cervical the distinction between tuberculum and capitulum becomes gradually lost. With this simplification there takes place a reduction of the transverse process, which, never strong, disappears in the anterior sternal region, and, as pointed out by Osawa (98^a. p. 735), is formed by

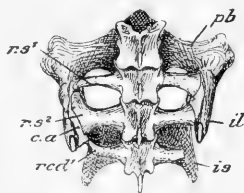
¹ At the outset of our investigation into the "cervical" region, mindful of the belief in the Chelonian affinity of Sphenodon and the assertion by W. K. Parker ('Challenger' Reports, Zoology, vol. i. pp. 47 & 50) that in the embryo of the Green Turtle the somatomes of the neck and tail are more numerous than later, and undergo numerical reduction by abortion, we kept a look-out, in vain, for probable evidence of a similar process, so far as it might involve the skeleton in Sphenodon, in the hope of being able to obtain some clue to the meaning of the numerical variation of the reptilian præsternal segments so conspicuous among the Dolichosauria and Mosasauria. From the discovery of facts concerning the variation in relationship of the sternum which we herein describe (*infra*, p. 34), we are disposed to regard numerical variation among the præsternal vertebrae, if not the poststernal also, as associated rather with a shifting of the sternum than an excalation of segments, as Parker's allegation would seem to suggest.

both the centrum and the arch. Günther describes the heads of the ribs as "low and compressed," and attributes to them a wholly central articulation. Baur has more correctly shown (86. p. 735) that the connection is rather with the arch, but he nevertheless insists that "in reality the rib never completely forsakes the centrum."

We can confirm the details of Baur's description and extend them to Stage S.

Of the so-called "lumbar" ribs, *i. e.*, the posterior two to four of the præsacral series, the head of the last one may show increased expansion, and in this way that may become in a sense transitional to the sacral rib, the special feature of which (Pl. II. fig. 5, *r.s.*) is its general robustness and greater attachment to the centrum. Except to point out that the sacral ribs are ossified in the manner of the præsacral (Pl. II., *cf.* figs. 4 & 5), we have nothing to add to recorded descriptions concerning them. There are usually two pairs, of which the anterior are the more slender and transversely disposed, the posterior the more robust and forwardly directed (Pl. I. fig. 12, *r.s.*). The iliac articulation is usually furnished by their united outer cartilaginous extremities.

Fig. 6.



Sacrum with hip-girdle of an adult *Sphenodon*, bearing on the left side an abnormal set of ribs.

c.a., articular cartilage; *il.*, ilium; *is.*, ischium; *pb.*, pubis; *r.cd.*¹, first caudal rib;
*r.s.*¹, *r.s.*², sacral ribs. Nat. size.

In view of the frequent existence of three sacral ribs in many living Lacertilia¹, of more than two in the Chelonia, of the occasional presence of a third in recent Crocodilia², and particularly of that of at fewest three pairs in Palæohatteria³, interest attaches to a skeleton preserved in the Dublin Museum of an adult *Sphenodon* (text-fig. 6) having on the left side a trisegmental sacrum, on the right a sacrum and hip-girdle normal in all respects. The third sacral rib on the left (*r.cd.*¹) is seen to be the first caudal, enlarged and expanded. Externally it was in life continuous by its outer

¹ Stollé and Chamæleo, Credner, H.: *op. cit.* p. 505. Phrynocephalus, Cope, E. D.: Proc. Amer. Philos. Soc. vol. xxx 1892, p. 207. For other examples *cf.* Siebenrock, F.: Ann. naturhist. Hofmus. Wien, Bd. vii. p. 373, and Sitzb. Akad. Wiss. Wien, Bd. civ. p. 67.

² Baur, G.: Zoolog. Anz. Bd. xii. 1889, p. 240.

³ Credner, H. *op. cit.* p. 505.

cartilaginous border with that of the second sacral rib. This was stouter than usual, while the first rib, reduced externally to a degree proportionate to the extension of the first caudal into the sacrum, was reduced to the calibre of a præ-sacral rib. The combined cartilaginous heads of the three ribs, by union, furnished the iliac articulation, and there can be no doubt that the determining cause of this abnormality was the backward rotation of the left ilium, well marked. It may be a case of "vertebral assimilation"¹, but its interest is none the less if so.

We have only to add, concerning the caudal region, that at Stage S, when ossification is setting in, the detailed relationships of the caudal rib to its centrum and arch are closely identical with those of the sacral vertebræ (*cf.* Pl. II. figs. 5 & 6), and that at this stage comparison with the præsternal region (fig. 4) shows that the interarticular tissue between the rib and its vertebra is far less differentiated than there.

The most conspicuous difference recognizable on a survey of the whole series of rib-heads in the adult and the later developmental stages of *Sphenodon*, is the fact that while the individual rib is for the most part obliquely attached or articulated upon the anterior end of its related centrum, in the case of the third and fourth præsternal ribs, which are two-headed, this antero-ventral extension is more marked and involves the intercentrum, the capitular head abutting against that. For this an explanation has to be sought.

Examination of the posterior trunk, sacral, and tail vertebræ, at the period of chondrification, would seem to indicate (*cf.* figs.) that the ribs arise only in relation to the vertebral bodies, and that they may be derivative of either their arch system, as originally believed for the higher Vertebrata by Gegenbaur, Goette, and others; or of their transverse processes, as argued by Claus, and more recently by Corning² and others—*i. e.*, that in any case they would appear to be vertebral in origin, as has been more recently maintained for the ribs of the Vertebrata generally by Dollo³. Hofmann, in a memorable paper published in 1878⁴, from the study of both the anatomy and development of adequate representatives of all the amniote classes but birds, deduced the final conclusion that the ribs of these animals are primarily intervertebral. Baur has further sought to support this view⁵, and Gadow, among most recent investigators, has done likewise, in his final conclusion (96. p. 50) that the ribs of the Amniota are lateral outgrowths and the chevrons and hæmapophyses ventral outgrowths of his "basiventralia," which give rise to the intercentra⁶.

¹ *Cf.* Siebenrock, F.: Ann. naturhist. Hofmus. Wien, Bd. vii. 1892, p. 373.

² Corning, H. K.: Morph. Jahrb. Bd. xvii. 1891, p. 611; *cf.* also Goeppert, *ibid.* Bd. xxv. 1897, p. 247.

³ Dollo, L.: Bull. Sci. Fr. & Belg. tom. xxiv. 1892, p. 113. For other references, see Hofmann, *infra*.

⁴ Hofmann, C. K.: Niederl. Archiv, Bd. iv. 1878, p. 199.

⁵ Baur, G.: Amer. Nat. vol. xxi. 1887, p. 942.

⁶ Psychologically interesting in this association is the conclusion of Dollo (*op. cit.* p. 128), who, though apparently in error concerning the vertebral origin, regards the "ribs" as dorsal ribs, the "hæmapophyses" as ventral.

On examination of transverse sections through the developing vertebral column of *Sphenodon* at Stage P, at which the parts of the cartilaginous vertebrae are as yet undifferentiated, the tissue giving rise (Pl. I. figs. 3 & 4) to the paired intercentra (*i.p.*)—which, it will be remembered, are the first, and at this stage the only components of the vertebral column recognizable—is seen to be continuous with that differentiating into the ribs (*r.cd.*). Figs. 3 and 4 represent the first and sixth sections across an individual caudal segment; and comparison of those which intervene has shown us that even here, when the vertebral body is not yet differentiated, the disposition of the proximal end of the rib is oblique, involving ventrally and anteriorly the intercentrum, dorsally and posteriorly the region of the future centrum and arch. Comparison with the adult cervical rib reveals a close similarity of relationship; and since with later development the connection with the intercentrum is lost, the primary relationship of the rib is proved to be intervertebral.

Cope in 1878 first drew attention¹ to the existence in certain Permian Pelycosauria of a two-headed condition of the rib, with accompanying intercentral articulation of the capitulum; and Baur, eight years later, in his afore-mentioned paper on the cervical ribs of *Sphenodon* (prompted by Cope's announcement), sought to emphasize the importance of this. Cope, immediately afterwards, in dealing with the structural resemblances between these creatures, prompted by Hofmann's brilliant generalization afore-mentioned, penned the remarkable paragraph²: "The passage of time has seen in the Reptilia generally" a modification "in the mode of attachment of the rib," in which, "in passing from front to back, the intercentral articulation is lost, and finally the head of the rib disappears." The facts we have just described render this well-nigh prophetic; and it remains to be ascertained how far the supposition, deduced from the study of longitudinal sections alone, that the ribs of the Amniota, and of the Reptilia in particular, arise in exclusive relationship to the transverse process, centrum, or arch, will stand the test of examination in other planes, and, as deduced from that of developmental stages at which chondrification is more or less advanced, will bear further comparison with the earlier ones of procartilage differentiation.

Concerning the bodies of the ribs, we have nothing to add to the descriptions of Günther, Maurer (96), Osawa, and others, except as regarding the so-called "uncinate processes." Günther in his original description accords the first of these to the last præsternal rib, Osawa to the penultimate, but neither state their posterior limitations. Like those of the Ratite birds, they are apt to be easily lost in maceration; but in carefully prepared specimens we have been able to trace them back, with

¹ Cope, E. D.: Proc. Amer. Philos. Soc. vol. xvii. 1878, pp. 518 *et seq.*; and Proc. Amer. Assoc. Adv. Sci. 1884, pt. ii. p. 474.

² Cope, E. D.: Trans. Amer. Philos. Soc. vol. xvi. 1886, p. 249.

progressive diminution in length, to the 11th-12th poststernal rib. They are longest throughout the middle of the series, and they arise late at Stage Q, after the ribs have become chondrified, by independent concentration of the cells which go to form the intermuscular septa. They also chondrify independently at Stage R (Pl. II. fig. 7, *u.p.*), at which the ribs are well ossified. Jeffery Parker has already called attention¹ to their similar independence in Apteryx, and we accordingly follow him in the usage of the term *uncinates*.

There can be no doubt that the process borne by the last præsternal rib is a true uncinete, since our sections at Stages Q and R reveal its independent origin. We find that the "process" borne by the penultimate rib, which Günther (67. p. 607) believed to be homologous with the uncinates and which Osawa definitely refers to them, may by elongation assume the size and shape of one in its most pronounced form, as contrasted with its condition described by Günther of a mere "dilated hæmapophysis." On the study of this he was led to regard the uncinates as hæmapophyseal in origin, "separate and removed from the distal end of the pleurapophyses as the latter increase in length." At our Stage R, at which the ribs are beginning to ossify and the uncinates proper are still distinct from them, the penultimate rib and its supposed uncinete are continuous, while a similar but feebly developed process is present on the antepenultimate rib. At the period of continuity, the penultimate rib and process may in some sections present appearances suggestive of a possible precocious union; but, inasmuch as we are unable definitely to detect its presence at an earlier stage or in a wholly free state, we leave it an open question whether the "process" may or may not be a mere outgrowth of the cartilaginous rib. If the non-extension of the osseous rib into the uncinete zone be due to loss of connection with the sternum, the former conclusion would be the more likely; if, on the contrary, it be not so, it may well be that, under the extension of the unossified moiety into the zone, the plastic cartilage has been seized upon as available for extension and support under the mechanical conditions at work.

The Sternum.—By way of descriptive detail, of the adult sternum we have nothing to add to the statements of Günther and Osawa, except to state that neither has recorded the fact that even in the adult its posterior border is notched. At Stages R and T this notch (Pl. VI. figs. 5 & 6, *s.n.*) is very conspicuous, and inasmuch as at Stage Q the two halves of the sternum are widely separated, the question arises whether or not the notched region is one of non-union of its opposite halves.

Parker, in describing the developing sternum of Apteryx, in the adult of which there are four pairs of sternal ribs, has shown² that the two anterior of these apparently give rise to the sternum, and that the connection of this with the two posterior is secondary and due to extension of both sternum and ribs. In *Sphenodon* three pairs

¹ Parker, T. J.: Phil. Trans. 1891 B, p. 80.

² Parker, T. J.: *op. cit.* cf. pp. 87 & 113.

of sternal ribs have been hitherto described for the adult, but we find that four pairs may be present, as, for example, in a skeleton in the Teaching Collection of the R. College of Science, Dublin. Similarly, in the developmental stages, four pairs may occur, as at Pl. VI. fig. 6 (Stage T), or four on the left side only, as at Pl. VI. fig. 5, or on the right, as in specimens of Stage S in our possession.

The earliest developmental stage of the sternum we have observed is at Q. In the section of this figured (Pl. VI. fig. 4) but two ribs are seen to contribute to the sternum, but examination of serially related sections proves that the third enters also into its formation; and, from what we have seen, we incline to the belief that when a fourth is present it also has contributed.

In the latest stage figured, the organic continuity between ribs and sternum is still uninterrupted, the "*incisuræ costæ*" being of late origin. As early as Stage R the *sulcus coracoideus* (*cor.*) is well indicated, and anteriorly the sternal plate is prolonged into a couple of episternal cornua, which skirt the stem of the interclavicle and contribute to the formation of the sulcus, in a manner which holds good for the adult, but has been inadequately recognized in all previous descriptions.

In the specimen from the Dublin Museum, this last right præsternal rib reaches the sternum, and its cartilaginous segment, by elongation and enlargement, has the characters of a normal sternal member. Its osseous segment is normal, and there are no accompanying changes recognizable in the ribs in front of it. We have already adverted to one point of interest attaching to this specimen (*antea*, p. 30); and if, as there is reason to believe from what is known of the Mesozoic reptiles, the amniote sternum in its ancestral condition, in which it was most certainly cartilaginous, was more extensive than its more specialized homologue of the living forms¹, fluctuation anteriorly and posteriorly such as we have recorded becomes the more readily intelligible.

There are no indications of any elements, median or otherwise, entering into the composition of the sternum, beyond those derivative of the ventral extremities of the ribs.

The "Abdominal Ribs" (Gaстрalia²).

These are in number 22 to 26, and they are alternately attached to the ventral segments of the poststernal ribs and free, at any rate for the most part, as originally pointed out by Günther. Osawa records 24, of which he remarks the first is attached to the first poststernal rib (98. p. 491), as are those behind corresponding to odd numbers, back to the 21st. The 22nd, 23rd, and 24th, with those corresponding to even numbers, he describes as free. We find, however, that regarding the first point there

¹ Osborn has described fossil an expanded cartilaginous sternum arising from ten pairs of ribs in the Mosasaur *Tylosaurus dyspeltor* (*op. cit.* [*antea*, p. 14] p. 180).

² Baur, G.: *Anat. Anz.* Bd. xiv, 1897, p. 150.

is considerable variation. Boulenger has called attention¹ to the fact that "the anterior extremity of the plastron overlaps the posterior extremity of the sternum," and concerning this, two specimens we have examined yield interesting results. In each of them there are two free gastralia in front of the first that is attached to the ribs; and while in one example (that possessed of four pairs of sternal ribs) these are short and median, in the other (that in which the last "cervical" rib is sternal) the anterior gastridium is represented by a symmetrically-arranged pair of rods.

Günther originally described each gastridium as of three elements, and their natural relations are generally those indicated in Pl. II. fig. 10, no. 7. Not unfrequently union in the middle line, as figured and described by him, may occur, and it would seem to involve a forwardly-directed spur on the median element which is generally present (*cf.* Pl. II. fig. 10, no. 11). Much interest attaches to Günther's description of an exceptional specimen, in which for the rib-connected gastralia the lateral elements were attached to the central by transverse "joints," instead of being in oblique juxtaposition with them as for the free gastralia and as is more generally the case throughout the entire series. The fact that, in most specimens we have examined, individual gastralia of both the attached and free order show both "jointing" and juxtaposition, and that while in most cases one or two such "joints" may be present only on one side—there being no regularity recognizable,—proves that no physiological significance is to be attached to these variations.

Turning to the embryo, we find that the gastralia arise at Stage S, within previously differentiated fibrous tracts of the subcutaneous tissues of the body-wall (*g.t.*, Pl. II. fig. 9), by a process of calcareous deposition, which proves them to be wholly membranous in origin. Their connection with the myocommata of the body-wall is fully established later, and with Gadow² we have failed to detect any traces of a cartilaginous origin, believed by Schneider to be the case for the Crocodilia. Figs. 8 and 9 represent (8) the anterior (third to fifth), 9 the posterior (16th to 18th and more highly magnified) gastralia of an example at Stage S. It will be observed that the median element is present only anteriorly, and that while for two of the three segments figured comparison with the adult shows its lateral cornua to be partly represented by a series of minute calcifications, for the anterior segment it is composed of two pieces. Anteriorly the lateral elements are seen to be fully formed, but on passing to the posterior series two of the three figured are observed to be represented by a linear series of distinct calcifications, the median element being undeveloped. The fact that in the adult the gastralia which occupy the positions of those here figured are alike symmetrical and only trisegmental, proves that with advancing development a union of the calcifications such as are here figured must occur, and that the median elements

¹ Boulenger, G. A.: Brit. Mus. Cat. Chelonia, Rhynchoceph. & Emydos. 1889, p. 1.

² Gadow, H.: Morphol. Jahrb. Bd. vii. 1882, p. 77.

arise antero-posteriorly. It further indicates a compound origin for all the parts, median and paired alike; and concerning the anterior paired segments, which in the individual figured were single, we find that in younger individuals at the same stage they may be represented by a series of elements. The details point to the conclusion that union is rapid and irregular.

A striking characteristic is this irregularity of calcification! It leads to irregularity of union; and it is fair to assume that in this lies the explanation of the asymmetry which the parts of the adult "plastron" are apt to assume. It explains the not infrequent presence of but a single asymmetric element, and of so extraordinary a condition as that of the triradiate or quadriradiate union delineated on Pl. II. fig. 10 (Stage T)—the most erratic we have observed. It also renders clear the substitution of transverse "joints" between, for oblique juxtaposition of, the median and lateral elements described by Günther, and the co-existence of these herein recorded, while it presupposes other combinations yet to be discovered.

Interesting and unexpected as are these details ontogenetically, we have come to attach a still greater importance to their probable phylogenetic significance.

One of the most distinctive characters of Credner's Palæohatteria of the Permian is the multisegmented condition of its "abdominal ribs," which, on careful examination of the originals, he has shown to be also the condition in Von Meyer's famous Proterosaurus and other genera to which he refers (*op. cit.* p. 538). In view of the obvious similarity to the embryo Sphenodon suggested, it becomes the more interesting to find that whereas in Palæohatteria, according to Credner's original description, there appear to have been three rows of calcifications present for each rib, in Proterosaurus there were two or three. In a later paper, however, on Kadaliosaurus, an allied genus, he gives¹ the number of "abdominal ribs" as regularly six for each vertebral segment possessed of them; and in instituting comparisons with Palæohatteria, Proterosaurus, Stereosternum, and Hyperodapedon, he gives the number present in them collectively as from three to six. The calcifications in all these forms are regular and structurally constant, whereas in Sphenodon they are developmentally irregular and inconstant.

Kadaliosaurus is further interesting in the light of the foregoing observations upon the substernal extension of the "gastralia" in Sphenodon, as in it they are still more nearly pectoral in extent and Stegocephalian. The facts suggest that the "plastron" may be undergoing reduction in the living genus, a consideration which may perhaps explain the irregular mode of calcification by which it is formed.

Boulenger, availing himself of these facts of palæontology, has made them a basis of classification of the Rhynchocephalian Order to which we alluded at the outset (*antea*, p. 3), and he has drawn a sharp distinction between the higher suborder of the Rhynchocephalia vera (91. p. 171) (Hatteriidae, Homeosauridae, Rhynchosauridae,

¹ Credner, H.: Zeitschr. deutsch. geolog. Gesellsch. Bd. xli. 1889, p. 330.

and Sauranodontidæ), characterized by the triserial condition of the "abdominal ribs," and the lower or Proterosauria (Palæohatteriidæ, Proterosauridæ, and Champso-sauridæ), in which their segmentation is multiserial. The adult Sphenodon, if classified by its "plastron," can only be referred to the former—the developing Sphenodon might with justice be relegated to the latter and lower suborder! In this, Boulenger's far-sighted classification receives welcome support.

Moreover, the multisegmented condition of the "plastron" segments is nothing short of a Stegocephalian character.

The Skull and Visceral Arches.

In compliance with passing custom, we have adopted in this section of our work the reconstructional method, as before stated (*antea*, p. 7).

Beyond the memoirs of the late Kitchen Parker, and some recent preliminary notes by Gaupp, together with the observations of Leydig (*op. cit.*), Born, and Hofmann, duly mentioned by him, little has been written upon the actual development of the Lacertilian chondrocranium¹; and since in the absence of figures we find it difficult to follow the details of Gaupp's descriptions, we deem it more prudent to describe connectedly the processes taking place in Sphenodon, which are simple and straightforward, and highly instructive in themselves.

The Chondrocranium.—In Sphenodon the cartilaginous elements of the skull arise before those of the greater part of the vertebral column, and the ossifications in membrane before those in cartilage of both skull and vertebral column. The first differentiation to form the primordial cranium which we have observed is at Stage P, and it consists mainly of pro-cartilage. It can be resolved into two perfectly distinct portions, excluding the mandibular arch—an anterior common to the olfactory and the trabecular regions, a posterior involving the sphenoccipital and auditory regions². Dealing with these individually, the anterior portion is seen to embrace the trabeculæ (Pl. III. figs. 1 & 2, *tr.*) and an ethmoidal constituent, consisting of an extensive basal plate with two pairs of outgrowths—an anterior or olfactory pair (*u.e.*) and a posterior pair—to be hereafter termed the *ethmosphenoidal plates* (*e.s.*). The trabeculæ (*tr.*), widely separated and enclosing a spacious pituitary foramen (*py.*'), are already hyaline, and pass gradually into the lateral edges of the basal ethmoid. The

¹ Gaupp, E.: Verhandlg. anat. Gesellsch. Sammlg. v. (Anat. Anz. Bd. iii., Suppl.) pp. 114, 120 (1891), also ibid. Sammlg. xii. (Anat. Anz. Bd. xiv., Suppl.) pp. 157-163 (1898), and Ber. naturf. Gesellsch. Freiburg i. B. Bd. x. pp. 302-316 (1898).

² Left uncoloured in our illustrations. Concerning the embryo which furnished the sections for figs. 1 to 3, Pl. III., it is regrettable that before investigating it we had handed it on to another, who, in decapitating it for other use, had cut through the auditory region. We found, however, on examination of slightly younger specimens, evidence sufficient for the extension of the differentiation into pro-cartilage into the regions included in the dotted lines in the figs.

posterior portion, at this stage disposed at right angles to the anterior (its anterior extremity being alone visible from above, as in fig. 2), is seen to similarly consist of a basal or parachordal plate (*par.*) also bearing two pairs of outgrowths, viz. an anterior (*o.s.*), to be hereafter termed the *otosphenoidal plate*, and a posterior, the auditory capsule (*c.au.*). This posterior portion is hyaline only at the anterior and lateral borders of the parachordal plate, the anterior chondrification extending into each of the otosphenoidal tracts. The intracranial notochord, enclosed within the basal parachordal plate, terminates anteriorly in a minute freely-exposed apex (*nc.*, fig. 2), and, as already pointed out by Dendy for Stage N (99^a. p. 75), it takes a sinuous course.

Dismissing for the present the sensory capsules, which at this stage are simple and cup-shaped, it becomes necessary for comparison of later stages to deal fully with the ethmo- and oto-sphenoidal plates. The former (*es.*) are large and wing-like and bear no outgrowths. The latter are complex and wholly distinct from the trabeculæ. Each of these otosphenoidal plates is seen to be extending upwards and outwards, backwards and inwards, and directly forwards. Two apertures are enclosed by it—a lower (*f. iii.*), which transmits the third cranial nerve, and an upper (*f. iv.*), which transmits the fourth¹. The processes to which it is giving rise (indicative of differentiation along definite lines) are five in number (*os.*¹ to *os.*⁵, Pl. III. figs. 1, 2, 3).

Before passing on to a later stage, we wish to emphasize the simple rod-like condition and non-extension into the cranial wall of the trabeculæ, which, except for their connection with the procartilaginous basal ethmoid, are disposed serially with the mandibular arch (*pg.mk.*).

At Stage Q, despite the short advance in time upon P, remarkable progress is seen to have been made in the formation more particularly of the cranium, nearly all the definitive components of which are now recognizable. The trabeculæ have now fused posteriorly with the parachordal—not by their ends as might be supposed, but by their postero-internal borders,—and they appear to us now to give rise to the basiptyergoid outgrowths (*bs.*, Pl. III. fig. 6). An accompanying upward rotation of the parachordal (associated with cranial flexure) has brought about a consequent approximation of the otosphenoidal plates to the trabeculæ, with an accompanying fusion involving the first and fifth otosphenoidal processes. Of these, the latter, passing downwards, unites with the outer trabecular border, and thereby shuts off (*f.j.*, fig. 4) a jugular foramen; the former, uniting with the inner trabecular border, encloses a passage (*f.a.*) for the ophthalmic artery.

More significant than the foregoing is the change in position undergone by the second and third otosphenoidal processes. Originally directed upwards, under the combined influence of rotation and growth, they are now directed forwards, and, by union with the posterior border of the sphenethmoidal plate, they have come to bridge longitudinally the membranous lateral cranial wall. As the result of this, two

¹ Gaupp (1898, Berichte, p. 8) describes these nerves in the Lacertilian as related to a common fenestra.

further fenestræ arise in the same vertical plane in front of those already described. Of these the upper or *lateral cranial fenestra* (*f.n.*, Pl. III. figs. 4, 6, 7) is wholly membranous, transmitting nothing, the lower (*f.ii.*) giving passage to the optic nerve. It will further be noted that with the establishment of this union between the ethmo- and otosphenoidal plates the parts most nearly related to the latter have become expanded and carried up by growth of the basi-ethmoidal plate, together with which they constitute a considerable cartilaginous interorbital septum.

The fourth otosphenoidal process, originally directed downwards (*os.*⁴, fig. 1), now carried up, looks straight backwards (*cf.* figs. 5 & 8), but it has remained free.

On appreciation of these important processes, which have effected so marked a change in the configuration of the parts, it is evident that growth must be most rapid in the otic border of the otosphenoidal plate.

The chondrocranium at this stage, viewed from beneath, reveals changes which, though less dominant than those described above, are in themselves remarkable. Massive indeed have the basis cranii and auditory capsules become, under the accelerated growth associated with the straightening of the basi-cranial axis and the marked lateral expansion of the post-pituitary floor (*cf.* figs. 6 & 7). The occipital region has now become conspicuous, by the upgrowth on either side (*eo.*, Pl. III. figs. 6 & 7) of a considerable cartilaginous lobe lying free of the auditory capsule, between which and it there lies the huge interspace for the 9th, 10th, and 11th cranial nerves (figs. 6 & 7, *f. ix. to xi.*).

Anteriorly to the trabeculæ the basal ethmoidal plate (*cf.* fig. 6), vertically extended as has been seen, has undergone a forward growth—as is proved by the fact that its length is now as great as that of the trabeculæ themselves, and it has also undergone a downward rotation, very marked as viewed from the side (Pl. III. fig. 4).

The pituitary foramen at this stage (*py.*¹, Pl. III. figs. 6 & 7), compared with that of Stage P, as represented in the accompanying figs. (*cf.* fig. 2), would seem to have undergone considerable reduction with advancing growth. When, however, it is remembered that the figure of Stage P (fig. 2) is magnified 13 times, that of Q (figs. 6 & 7) but 8, it will be evident that under the growth-changes going on the trabecular tracts which more directly bound the foramen have been well-nigh stationary, and that such reduction of the foramen as has taken place would appear to be rather due to the mode of union between the trabeculæ and parachordal cartilages than to actual cartilaginous invasion.

Finally, as to the sense-capsules—now both chondrified. With the olfactory capsule complication has set in. Its capsular portion (*nc.*) has entered into a union with the anterior border of the ethmosphenoidal plate, giving off dorsally a short *supranasal process* (*nc.*¹, fig. 4) connected with the plate by an *ethmonasal bar* (*eb.*) lying within the outer border of the olfactory nerve foramen. At its anterior extremity it gives off a *prænasal process* (*nc.*², fig. 4), which embraces the anterior wall of the nasal sac.

Somewhat similarly related to the postero-external wall of the sac is a large quadrangular cartilage, the *extranasal* (*ex.*), and from this four processes arise. The two anterior of these (*ex.* 1 & 2) are united to the ethmoidal bar so as to enclose a fenestra (*n.f.*¹). The two posterior are free, and the third (*ex.* 3), together with the posterior half of the parent cartilage, disposed at a sharp angle to the external half of this, contributes to the support of the anterior orbital wall, bounding ventrally the ethmoidal foramen (*f.e.*), which transmits the ophthalmic branch of the fifth nerve ¹.

In addition to these complex nasal supports, there is present at this stage in the nasal floor a sheet of procartilage which, in order to complete our terminology, we name the *subnasal*. This, to which we shall return, is wholly independent in origin, and by analogy to the extranasal we suspect that this may also arise independently.

The only remaining changes in the chondrocranium are mainly of the nature of advancing completion of the parts now described. No new elements are added after Stage Q. These perfecting processes, as they may aptly be termed, are most conspicuous at Stages R and T, which may accordingly be dealt with independently.

Stage R.—A very striking feature of this, as compared with the earlier stages, is the straightening out of the ethmosphenoidal region, which at Q was downwardly rotated (*cf.* Pl. III. figs. 4 & 8). This straightening process affects most conspicuously the median parts (internasal septum), which now appear as if withdrawn under cover of the extranasal cartilage (*ex.*, fig. 8).

Equally striking are changes involving the antorbital and otoccipital regions. That taking place in the former is of the nature of extension most markedly dorsalwards of the interorbital septum (*s.i.*), by continuation of the process of elevation of the basal ethmoid already alluded to (*antea*, p. 39). Under the combined influences at work, growth has become more rapid with the ethmosphenoidal than with the otosphenoidal plate; and ready proof of this lies in the now upward direction of the third otosphenoidal process (*os.*³, fig. 1), which at Stage Q (*os.*³, fig. 4) was arched and reached the highest point. Of the fenestræ described at Q (which in life are closed by membrane, except where they transmit nerves) only one has undergone change, viz. that transmitting the fourth cranial nerve (*f.* 4, fig. 8). This is now complicated, having become continuous with the fenestræ transmitting the third cranial nerve, the jugular vein, and ophthalmic artery—all four being now closed by one continuous membranous sheet. It is clear, on comparison with Stage Q, that the cartilaginous bridges which originally separated these fenestræ (*i. e.*, the fifth otosphenoidal cartilage and its near neighbours) have been absorbed.

As an accompaniment of these changes, the small cartilaginous bar bounding at

¹ *Cf.* Osawa, 98^a, p. 504.

Stage Q the front of the foramen for the fourth nerve has become much elongated and brought into line with the second otosphenoidal process, so as to give the appearance of a continuous bar. That this is not the case, however, is proved by the fact that the second otosphenoidal process in reality is now represented by the insignificant tract (fig. 8, *os.*²) lying between the ventral extremity of the cranial fenestra (*f.n.*) above and the dorsal extremity of the optic fenestra (*f."*) below. Its apparent forward continuation at this stage is due to the appearance in the cartilaginous interorbital septum of yet another fenestra (*f.i.*, Pl. III. fig. 8), which is of necessity median. Like the lateral cranial fenestra (*f.n.*), it is wholly membranous, and it alone merits the term *interorbital fenestra*.

Turning to the occipital region, the foramen magnum is now seen to be completely surrounded in cartilage, as the result of union between the upper ends of the occipital cartilaginous lobes and the posterior walls of the auditory capsules, resulting (*cf.* Pl. III. fig. 9, *e.o.*) in the enclosure of the afore-mentioned interspace transmitting the cranial nerves ix. to xi. above, and its conversion into a foramen. With these changes another, probably correlated with the afore-mentioned upheaval of the ethmosphenoidal plates, is recognizable, viz. the appearance in the postero-dorsal cranial roof of a spatulate cartilage (*so.*¹, Pl. III. figs. 8 & 11), which in its general relationships recalls that figured and described by Parker¹ in *Lacerta* and *Zootoca* as "supra-occipital." This is seen to arise posteriorly from a massive tract of cartilage overlying the foramen magnum, which appears to us more extensively derived by the overarchng of the auditory capsules than of the occipital lobes. When the chondrocranium is viewed from the side, at this stage, this "occipital" cartilage is seen to be arched, and to follow, with the antero-dorsal border of the expanded ethmosphenoidal plate, the arc of the circle described by the top of the head, which at the earlier stage was followed by the third otosphenoidal process (*os.*³, Pl. III. fig. 5). In this respect, the two may be said to have been correlatively modified in accommodation to the roofing-in of the brain, now possible under the diminution in relative rapidity of the growth of the central nervous system.

An interesting detail at this stage is the presence in the basi-occipital region of a minute depression, involving the lower border of the foramen magnum. Conversely, the ventro-lateral border is on either side rounded and convex, the whole giving to the chondrocranium, especially when viewed from above (Pl. III. fig. 11) or from beneath (fig. 12), the appearance (as has been pointed out by Gaupp² for the embryo lacertilian) of being doubly condylar.

In the nasal region the extranasal cartilage (*ex.*, Pl. III. fig. 8) has increased in size, but it has undergone no conspicuous change, except for the elongation of the

¹ Parker, W. K.: Phil. Trans, 1879, p. 595.

² Gaupp, A.: 1898, Berichte, p. 6.

fourth of its processes (*ex.*⁴), which now lies in an interspace between the palatine and maxilla (*cf.* fig. X., *ex.*⁴)¹. The subnasal sheet (*sb.*), now chondrified, wherefore it may be termed the *subnasal cartilage*, has entered into continuity by means of a delicate cartilaginous bar with the prenasal process (*nc.*"') of the primitive olfactory capsule, and by a less considerable bar with the extranasal cartilage (*ex.*, fig. 8). It extends inwards, partly underlying the vomers, and effects (as indicated in fig. 12, *s.b.*) an infolding of the outer lip of the posterior nares.

Stage T.—At this stage the characters of the definitive chondrocranium are all present, and, owing to the increase in size, we found it unnecessary in dealing with it to resort to microscopic sections and reconstruction. Fig. 10, Pl. IV., delineates from the left side this chondrocranium, divested of all dermal elements except the parasphenoid (*ps.*), now co-ossified with the basisphenoid (*bs.*). The most conspicuous changes to be observed are two, (i.) the backward extension of the fourth otosphenoidal process (*os.*⁴) and its fusion with the auditory capsule at the base of the supra-occipital bridge, (ii.) the elongation of the ethmo-nasal region, which is a main factor in the final realization of the adult proportions and shape of the skull. As the result of the fusion above-named, the lateral chondrocranial wall is now in a condition of uninterrupted continuity dorsally with the olfactory and auditory capsules, and the passage transmitting the fifth cranial nerve now becomes a perforated fenestra. In proportion, size, and shape, the fenestræ have undergone a considerable amount of change, mainly associated with the cartilaginous extension of the interorbital septum (*s.i.*). By the extension of the lateral cranial wall, the process of closing in of the roof has advanced, but there is no change of importance as compared with the preceding stage.

The nasal capsule has become modified by the fenestration (*n.f.*"') of the extranasal cartilage.

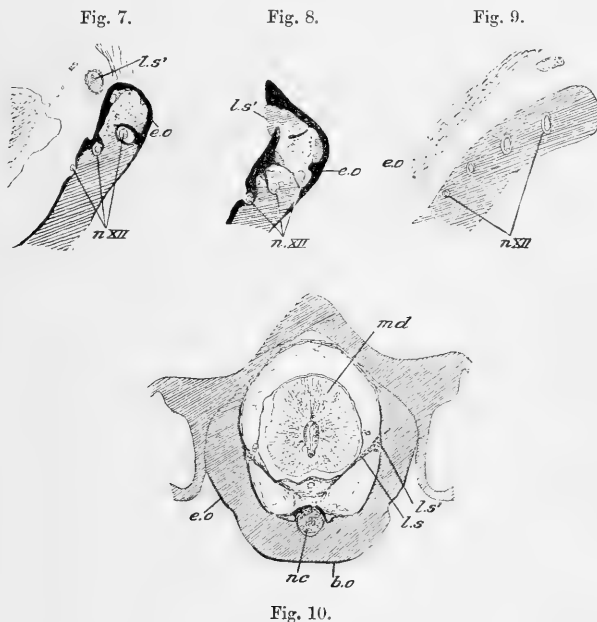
The cartilage-bones (which appear at Stage R, but, owing to their then feeble condition, are not represented in our accompanying figures of the models at that, figs. 9 & 12, Pl. III.) are seen assuming shape at S (figs. 4, 5, 6, & 7), but at T they are in the condition most favourable for description. They are 9 in all—3 median and 3 paired—and with the exception of the basisphenoid all are otoccipital.

When the skull is examined from beneath (Pl. IV. fig. 6) the basisphenoid (*b.s.*) and basi-occipital (*b.o.*) are seen to arise within the anterior and posterior regions of the post-pituitary floor. The former extends laterally into the cartilaginous basipterygoid processes (*bs.*)², which at Stage T terminate externally in dilated extremities, for articulation of the pterygoid bones; and it also extends forwardly into the trabecular

¹ This is presumably the "processus maxillarius posterior" of Gaupp, which he aptly compares with the "antorbital" or palatal bar of the Anura and Ranodon (1898, *Berichte*, p. 8).

² We have found traces in transverse section at Stages R–S of the paired ossification asserted by Baur (*Zool. Anz.* Bd. xii. p. 45) to hold good for the basisphenoid and stated by Parker to be present in the *Lacertilia* ('*Morphology of Skull*,' 1877, p. 216).

region, so as to enclose the pituitary foramen, now undergrown by the parasphenoid (*cf.* transverse section, Pl. IV. fig. 3). The basi-occipital (*b.o.*) arises from a single ossific centre. The exoccipitals arise as ossifications of the occipital lobes of the chondrocranium, and by extension reach the posterior boundary of the exit for the ninth to the eleventh cranial nerves. Osawa has recently described (98^a. p. 494), with perfect accuracy, the adult condition of the nerve-foramina which result from this, and concerning the hypoglossal foramina he gives two as the number present. He also describes



Figs. 7 to 10.—Sections through the occipital region of *Sphenodon* showing the hypoglossus nerve-foramina at different stages of development, and the sustentacular ligaments of the medulla. 7 and 8. Lateral longitudinal sections at Stage S, $\times 33$. 9. Lateral longitudinal section at Stage Q, $\times 67$. 10. Transverse section at Stage R, $\times 33$.

b.o., basioccipital; *e.o.*, exoccipital; *l.s.*, sustentacular ligament; *l.s'*, its exoccipital support; *md.*, medulla oblongata; *nc.*, notochord; *n. xii.*, hypoglossal nerve-roots and foramina.

two nerve-roots. Gaupp accords a third hypoglossal foramen to the embryo Lacertilian (Berichte, p. 5). Interesting this, in consideration of modern discovery concerning the truncal origin of the hypoglossal nerve-bearing region of the skull. Still more interesting when we record the fact that, whereas in *Sphenodon*, at Stage S, three hypoglossal foramina are present, with corresponding nerve-roots (*n. xii.*, text-figs. 7 and 8),

at Q (text-fig. 9) there are four foramina and five roots. It is certain that, during ontogeny, two roots at least disappear, and further investigation is necessary to render perfectly clear the detailed nature of those which remain¹.

We may most fittingly refer here to a series of ligamentous supports which, so far as we can ascertain, are new. We first detected them at Stage Q in the occipital region. At S each is very conspicuous, and with its fellow of the opposite side is closely applied to the under face of the medulla oblongata. It is strengthened at its bases by ingrowths of the occipital cartilage (*l.s.*¹, text-figs. 7, 8, & 10), and in the floor of the neural canal it enters into a loose fibrous connection with the dura mater (*cf.* fig. 10). This remarkable structure is repeated segmentally throughout the trunk-region of the vertebral column, and we propose to term it the *sustentacular ligament*.

The supra-occipital calls for no special comment.

The opisthotic (*op.*, Pl. IV. fig. 9), which Siebenrock has proved², to be an independent element (the "paroccipital" of Owen), is at this stage remote from both the prootic and exoccipital, and the ossific centre of the former is now beginning to monopolize the feebly-developed cartilaginous parotic process (*p.p.*), which appeared at Stage Q and is still short. The prootic ("otosphenoid," auct.) (*pro.*, figs. 8 & 10) is a simple bone, and its processus anterior inferior, so characteristic of the adult³, has not yet appeared, nor has ossification yet encroached upon the processus anterior superior, which, still hyaline, forms (*cf.* fig. 8, *c'*.) not only at this, but at Stages R and S, a formidable projection.

The Mandibular Arch.—This is first differentiated at Stage P, in the form of a minutely procartilaginous mass having a body or quadrate portion (Pl. III. fig. 1, *q.*) bearing three outgrowths: an antero-dorsal or pterygoid (*p.g.*¹), a postero-dorsal—the future epipterygoid (columella), *epg.*,—and an antero-ventral, much the stronger of the three, the Meckelian bar (*mk.*).

The main body or quadrate mass, at this stage somewhat squarish, is disposed parallel with the parachordal (*pc.*), and throughout the later stages, at which the rotation of the latter and the straightening out of the basis cranii already referred to are effected, it retains this relationship, *i. e.*, the absolutely distinctive characters of the whole arch are present in procartilage. Chondrification is seen to be setting in independently in its body and the Meckelian bar, and even at this early stage the latter is connected with its fellow symphysially by a thin procartilaginous tract. At Q advancing chondrification of the Meckel's cartilage invades the symphyseal tract, and the whole cartilaginous lower jaw becomes for the time a single hyaline mass. It remains such until Stage T, when the definitive symphysis begins to appear.

¹ *Cf.* Peter on *Ichthyophis* (footnote, *infra* p. 70).

² Siebenrock, F.: 1893, p. 304, English Transl.

³ *Cf.* Siebenrock, F.: Transl. cit. p. 307, & fig. 14, & Brühl, 'Zootomie aller Thier Kl.' pl. 149. fig. 5.

With advancing development, the chondrifying centre of the quadrate cartilage extends into the pterygoid and epipterygoid processes in common, and with this replacement there comes about the afore-mentioned rotation, under which the epipterygoid process, originally directed backwards and downwards, comes to be upwardly directed, the pterygoid bar being displaced accordingly. On the assumption of this rotation and its definitive position, the quadrate portion elongates and develops two processes—a dorsal or otic process (fig. 4, *q.*'), and a lower process, which appears correlatively with the segmentation off of Meckel's cartilage. Anteriorly its pterygoid portion turns suddenly outwards and expands (*cf. espec. Pl. III. fig. 6, pg.*'). Continuing to elongate, it comes at Stage R to overlies the pterygoid and the inner half of the os transversum, tapering to a point. Gaupp describes this cartilage in the Lacertilian as merely extending "in the direction of" the transversum. He points out (*Berichte*, p. 9) that did it continue forwards it would enter the maxillary region and that of the processus maxillarius posterior (our fourth extranasal process) of the nasal capsule, it would realize the condition occurring in *Ranodon* and the *Anura*. With this we fully agree; but we regard the extension over the transversum as indicative of the retention by *Sphenodon* of a more approximately batrachian condition than that thus far known for the Lacertilia.

In *Sphenodon* the study of the nerves and all possible relationships leaves no doubt that the epipterygoid process is the homologue of the processus ascendens of the batrachian quadrate cartilage, as recognized by Gaupp. He, however, seems to us somewhat in doubt¹ as to the actual occurrence in the Lacertilian embryo of a cartilaginous connection between the epipterygoid "Anlage" and the quadrate. In *Sphenodon*, so far from there being any doubt on this matter, not only are the epipterygoid and quadrate originally præformed in one continuous cartilaginous tract, but, from Stage R onwards, the portion of this which, after the establishment of these two bones, remains, begins to ossify by extension of the quadrate centre, to form the characteristic antero-dorsal quadrate lobe (*Pl. IV. fig. 11*), the presence of which accounts for the close relationship of the epipterygoid and the quadrate in the adult. The difference with the reduction of the jugal arch and the liberation and freedom of the quadrate associated in the Lacertilia is one in respect to which the gap between these and the Rhynchocephalia is immensely greater than between them and the Chelonia², to say nothing of the Crocodilia and other reptiles possessed of a fixed

¹ Gaupp, E., especially in his paper in *Anat. Anz.* Bd. vi. 1891, p. 107, and *Berichte cit.* 1898, pp. 9–11.

² We can only express astonishment, mixed with regret, at the gratuitous assumption by Osawa (98°, p. 102), in seeking to explain away the Güntherian dictum concerning the relationships of the quadrate to the pterygoid, that the latter arises from two ossific centres, of which the hinder has in *Sphenodon* become co-ossified with the quadrate. There is no trace of any such posterior pterygoid bone actual or potential.

quadrate. And in this connection it may be remarked that if the detailed configuration of the cartilaginous upper jaw be a criterion of relationship, the fact that a near approach to the condition occurring in *Sphenodon* is that of the Cæcilian *Ichthyophis glutinosa* as recently described by Winslow¹ is of great interest, when it is remembered that these Apodal Batrachia, in the possession of dermal ossifications and other well-known characters, are the most approximately Stegocephalian of all living forms².

The Hyoid and Columella auris.—Our observations concerning the hyoid apart from its connection with the auditory apparatus are few. At the earliest stage we have examined (viz. P) it has already appeared in procartilage in the form it assumes in the adult, except for slight differences in general proportion, as is better seen at Stage Q (Pl. III. fig. 4). We have no evidence pointing to a compound origin of its basal portion such as that described by Gaupp³ for the Amphibian, or of the complexity in structure of the order described by Siebenrock⁴ for the Chelonia.

It is only as concerning the vexed question of the relationship between the columella auris and the anterior cornu of the hyoid that we need proceed to details. The nature of this in the adult has been so oft recapitulated that it will suffice to point out once more that, apart from theories based on alternative interpretations of the facts of adult anatomy and surmises necessary for their defence, the real question developmentally at issue is whether or not the hyoid cornu and the extrastapedial are secondarily united, and whether the object called by Huxley suprastapedial does or does not arise independently.

Huxley, in describing the parts of the adult, regarded⁵ the whole columellar complex as hyoidean, and the extra- and suprastapedial processes as parts of its expanded outer extremity. Peters, and all subsequent investigators⁶, on the contrary, with the exception of Versluys, who has recently argued⁷ in favour of original continuity, have assumed that the connection between the extrastapedial and the hyoid cornu is secondary, while Peters more especially believed the suprastapedial to have been originally distinct. As great testimony to the extreme care with which Huxley worked at this problem, there stands the fact that he drew attention (*op. cit.* p. 398) to the presence, on the inner side of the foramen (*f.h.*, text-fig. 11, which for brevity's sake we associate with his name), of a fibrous differentiation included between the extra- and suprastapedial processes.

¹ Winslow, G. M.: Tuft's Coll. Stud. vol. i. no. 5, 1898, pl. iii. fig. 24.

² Cf. Boulenger, G. A.: P. Z. S. 1895, p. 402.

³ Gaupp, E.: Morph. Arbeiten, Jena, Bd. iii. 1894, p. 399.

⁴ Siebenrock, F.: Ann. naturhist. Hofmus. Wien, Bd. xiii. 1898, p. 424.

⁵ Huxley, T. H.: P. Z. S. 1869, p. 391.

⁶ Peters, W.: Monatsber. Akad. Wiss. Berlin, 1870, p. 15, and *ibid.* 1874, p. 40. Cf. also Baur, G.: Biol. Centralbl. Bd. vi. 1887, p. 655; Killian, G.: Jen. Zeitschr. Bd. xxiv. 1890, p. 649; Osawa, G.: 98^a, p. 520.

⁷ Versluys, Jan.: Zool. Jahrb. Anat. Abth. Bd. xii. 1899, p. 167.

Gadow alone among recent investigators has carefully examined a series of individuals, and he records further details. Chief among these is the discovery¹ that the Huxleyan foramen may be reduced to the size of a pin-hole or absent (*op. cit.* p. 467)—facts which point to the conclusion that its condition is indicative of variation in degree of extension of chondrification, especially when it is remembered that it transmits nothing.

Huxley described the head of the suprapedial process (p. 397) as connected with the parotic cartilage of the skull. Gadow, on the other hand, records in one example a ligamentous attachment to this; he remarks of another that "it does not touch the cranium" (p. 468); and of a third he writes, the hyoid is continued "along the anterior and lower margin of the extra-columellar cartilage, upwards to the parotic corner, when it does not fuse with, although it directly touches, the cranial cartilage." Sufficient this to show that the suprapedial is in its ultimate attachment variable.

With these facts in mind, we were especially attentive to the extrapedial region, and concerning it the following:—Examined at Stage S, and onwards to those stages in which the adult condition is assumed, lateral longitudinal sections through the quadrate (Pl. V. figs. 13 & 14) show that bone to be unossified dorsally. It is seen to be overlain by the squamosal (*sq.*), and when successive sections are followed outwards the extrapedial process (*e.c.*) is seen in the inner series to pass (Pl. IV. fig. 13) into the suprapedial (*s.st.*). As the sections become external the suprapedial is seen to approach the head of the quadrate and eventually to fuse with it, as in fig. 14 (*s.st.*), which passes through the Huxleyan foramen. Sections more superficial, as regarding the continuity of the parts, combine the appearance of these two figures. Examination of the whole series and dissection alike reveals (*cf.* Pl. IV. figs. 7 & 9) an absence of cartilaginous connection with the skull; and in the denial of this we are in agreement with Gadow.

The foregoing observations would at first sight appear contradictory to Huxley's. Examination of his fig. 4, however, reveals an error, in the fact that he has indicated as the exoccipital the parotic process of the opisthotic, as is proved by his delineation of its articular extremity. Allowing for this correction, his "parotic cartilage" can only represent the articular head of the quadrate; and, if so, his description amounts to that of a union between the suprapedial and the quadrate, such as we have described and have observed not only at Stage S but at T. And, as a consequence of this, it follows that cartilaginous continuity between the suprapedial and the skull does not exist, and that the quadratic union applies to the adult as well as to the young. Resorting to the earlier stages, with a view of ascertaining whether this union is or is not primary, we find in sections at Stage R that it does not

¹ Gadow, H.: Phil. Trans. 179 B, 1889, p. 468.

exist (*cf.* Pl. V. fig. 12), the quadrate head (q') and suprastapedial process ($s.st.$) being distinct though closely approximate. Passing to Stage Q (figs. 10 & 11), the distance between the two is seen to be much greater, the nearest approximation being that of fig. 11.

Turning now to the suprastapedial process, and the fibrous interval of Huxley. The former arises at Stage Q as a simple upgrowth, seen in section at fig. 10, Pl. V., *s.st.* When Stage R is reached, this is seen to be still elongating (text-fig. 11, *s.st.*) and to have given rise at the middle of its inner border to a recurrent process ($s.st'.$), which, passing downwards and inwards, becomes apposed to the columella auris ($st.$), to which it is tied by a series of fibres, which pass obliquely between the two. Between its recurved lower extremity and the columella a non-hyaline tract is present (*, fig. 12)

Fig. 11.

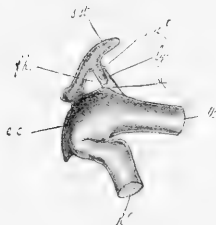


Fig. 12.

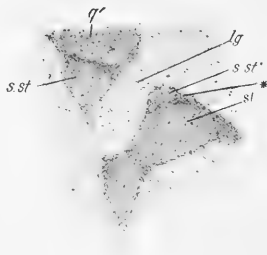


Fig. 11. Drawing from a reconstructional model, showing the detailed characters of the columellar head of *Sphenodon* and its derivative processes at Stage R, $\times 30$. Fig. 12. Microscopic section through the same, parallel to the columellar axis, $\times 75$.

e.c., extrastapedial; *f.h.*, foramen of Huxley; *h'*, anterior cornu of hyoid; *lg.*, ligamentous fibres; q' , upper end of quadrate; *s.st.*, suprastapedial; *s.st'*, recurrent process of the same.

which we conclude is that described by Huxley. It remains only to add that as the process is absent at Stage Q it is of secondary occurrence.

As to the continuity between the hyoid cornu and the outer head of the columella (extrastapedial process), we have evidence that for the earliest stages of differentiation (P especially), when all the parts concerned are in the procartilaginous state, it is complete; but a very interesting detail arises—viz., that in some of a series of thick sections which we possess there can be observed (Pl. V. fig. 5, *) a very feeble suggestion of jointing, so feeble that it would be likely to be overlooked by anyone not familiar with the sections. This, however, cannot be regarded as evidence of original discontinuity between the columella and the hyoid cornu! It is seen to be but a passing phase, indicative of either a probable ancestral or an incipient "jointing" such as takes place elsewhere along the cornu (**); and, as compared with a later

differentiation occurring at the base of the extrastapedial (Pl. V. fig. 12*b*), the primary independence of which has never been suggested¹, it is insignificant indeed.

Holding the foregoing facts proof sufficient that the columella, extra- and supra-stapedial are but the products of specialization of the upper extremity of the hyoid arch, with which they are at all stages continuous, we have in conclusion to direct attention to some puzzling procartilaginous tracts, of which we have been unable to detect a counterpart at a later stage. They are of the nature of two pairs of rounded masses (one of which is represented in Pl. V. fig. 1,†) disposed serially between the roof of the pharynx and the auditory capsule, ventrad of the fenestra ovalis region, and we are unable to hazard a guess at their significance.

Concerning the chondrification of the columella and the related anterior cornu of the hyoid, we find at Stage Q, when the procartilaginous tracts above described become hyaline, that all traces of the "jointing" disappear. Examination of figs. 6 to 9 (Pl. V.) shows this conclusively, and also that the hyoid cornu (*h.*) passes continuously into the extrastapedial (*ec.*), and through that into the columella (*st.*). The inner head of the latter, seen at the procartilaginous stage (Pl. V. figs. 3 & 4, *st.*) to merge into the feebly differentiated mass (*c.au.*) giving rise to the auditory capsule, at the period of chondrification is seen to be structurally continuous with that now hyaline, and in section (Pl. V. fig. 6, *st.*) delimitable only by a close approximation of its peripheral cells. Later, it becomes free, and attached to the rim of the fenestra ovalis by membrane, in the customary fashion (*cf.* Pl. V. fig. 12, *st.*). Its rod-like portion commences to ossify superficially, in the manner of the parts of the vertebral column and the otocipital bones.

The Trabeculae.—One very conspicuous feature of the afore-described stages in the development of the chondrocranium is the non-extension or incorporation of the trabeculae into the lateral cranial wall. As pointed out (*antea*, p. 38), these remain passive during the development of this.

Examination of the adult chondrocranium of *Sphenodon*, apart from a knowledge of its development, might well arouse the supposition that its fenestrae are due to absorption of an originally continuous wall, of the cartilaginous fish type. One of the most certain and fascinating of our results is the discovery that the cartilaginous cranial bars are all due to continuous-growth processes, that the correlated fenestrae are in no way due to absorption, and that the trabeculae play no part in the formation of the lateral cranial wall. From first to last these are simple rods, lost by union

¹ Kingsley, the latest worker who has dared to deal with the subject of the general morphology of the auditory ossicles (with which we are not concerned), expresses his conviction (Tufts Coll. Studies, No. 6, 1900, pp. 215-216) that the Lacertilian hyoid and columella are originally continuous in the embryo. He claims for the "extra columella" an independent origin, but since he uses the term in an unconventional sense and his figure (which does not bear out his description) leaves us in doubt whether his "extra columella" may not represent the supra-stapedial process, we feel justified in the above statement.

anteriorly with the basal ethmoid, united by their postero-internal extremities with the parachordal; and, what is more, they are serially disposed at all stages with the visceral skeletal arches.

Recent investigation by the reconstruction method has led to the conclusion that the developmental processes occurring in the skull of Man himself are not easily reconcilable with those generally believed to be passed through by even that of certain other mammals¹.

As is well known, Salensky in 1878 described² in the embryo Sturgeon a distinct cartilaginous centre for the lateral cranial wall; and Stöhr, in 1880, discovering that the parachordal of Triton³ appears in two pieces, in 1882 showed⁴ the basal portion of the chondrocranium of Rana to be complex, if not actually composed of three pairs of distinct elements—trabeculae, “mesotic cartilages,” and “occipital plates” (parachordals). Miss Platt has later described in Necturus⁵ the dorsal part of the “crista trabeculae” as paired, and instituted, on consultation with Sewertsoff, a comparison with the alisphenoidal cartilage originally described by him in Acanthias in 97⁶. While Peter, in the same year as Miss Platt, recorded the formation in Ichthyophis⁷ of so-called “dorsal trabeculae.” Most important of all, however, is the full monograph of Sewertsoff, which has appeared during the progress of our work, in which⁸, bringing the whole subject to a focus, he shows that in the Elasmobranch Acanthias the trabeculae take an insignificant share in the formation of the lateral cranial wall, and that this is mainly formed on either side from the above-mentioned distinct cartilages (termed by him the alisphenoidal), the pair of which, uniting with the trabeculae, contribute what he has termed the prochordal portion of the resulting chondrocranium. In his memoir he meets the challenge that if this cartilage be of the importance he claims, it should be more generally forthcoming, by showing reason for its being present in Pristiurus, that W. K. Parker had seen it in the Salmon⁹, and that other observers, and more particularly Miss Platt and Peter referred to above, had probably done so in other chordate forms. In view of this and of the similarity in posterior extension of the trabeculae along the parachordal in Acanthias and Sphenodon, and of the relationships of the latter to our otosphenoidal plate (Pl. III. fig. 1), we consider that this may perhaps represent Sewertsoff's alisphenoidal cartilage¹⁰.

¹ Levi, G.: Archiv mikr. Anat. Bd. lv. 1900, p. 407.

² Salensky, W.: Zool. Anz. Bd. i. 1878, p. 289.

³ Stöhr, Ph.: Zeitschr. wiss. Zool. Bd. xxxiii. 1880, p. 477.

⁴ Stöhr, Ph.: Ibid. Bd. xxxvi. 1882, p. 91.

⁵ Platt, Miss Julia: Morph. Jahrb. Bd. xxv. 1897, p. 377.

⁶ Sewertsoff, A.: Anat. Anz. Bd. xiii. 1897, p. 413.

⁷ Peter, K.: Morph. Jahrb. Bd. xxv. 1898, p. 555.

⁸ Sewertsoff, A.: Kupper Festschrift, Jena, 1899, p. 281.

⁹ Parker, W. K.: Phil. Trans. 1883, p. 129, pl. v.

¹⁰ During the passage of this Memoir through the press, Sewertsoff has announced details concerning the development of the skull in the Gecko (*Ascalabotes fascicularis*) which fully supports this conclusion (cf. Anat. Anz. Bot. xviii. p. 36, 1900).

Far reaching as is his discovery, and interesting as are its bearings on our own work, we venture to think that the most rational interpretation to be put upon the behaviour of the trabeculæ in *Sphenodon* is that of Huxley, originally put forward in his Hunterian Lectures in 1864, that they represent a pair of præ-oral visceral arches. Huxley reiterated this conclusion in 1874, in his suggestive note on *Amphioxus*¹, and von K  pffer gave it consideration and support in 1893², in his discovery of a pair of præ-oral visceral diverticula in the embryo Sturgeon. Further consideration of this very important topic is beyond the possibility of this memoir, but we hail with delight the discovery, as our work was nearing its termination, by von Davidoff, of the existence of this very pair of diverticula in the Lizards *Platydictylus* and *Lacerta*.

Cranio-facial Membrane-Bones.

The anatomy of these has been so fully dealt with by various authors, and most recently by Osawa (98^a. p. 497), that we have little to add to their descriptions. Developmentally, however, some interesting considerations arise. At Stage Q, the earliest at which we have been able to observe membrane-bones, the vomers, palatines, pterygoids, maxillæ, postorbitals, squamosals, angularia, supra-angularia, and dentaries are all present (Pl. III. fig. 5) and remote from each other. By the time that R is reached, all the membrane-bones present in the adult are represented (*cf.* Pl. III. figs. 10–12). Looking at the skull from the side, this does not at first sight appear so, but when examined fully it is found that while the frontals are approximated in the middle line, the parietals are widely divaricated and small and of a remarkable angulated type. Examination of the skull at this stage shows that the frontal and postfrontal, the præfrontal, maxilla, jugal, and postorbital are all in close relationship, first active development having apparently involved those elements which are circumorbital—a fact which immediately impresses itself on the mind when, at this stage, the skull is viewed either from above (fig. 11) or the side (fig. 10). And one is led to speculate how far this may not be indicative of a first protection of the eye, when it is remembered that the palæontological record proves the circumorbital

¹ Huxley, T. H.: Proc. Royal Soc. vol. xxiii. 1874, p. 131.

There is evidence among Huxley's unpublished notes that in the early 80's he was returning to this conception and to work upon the skull. He was bringing to bear upon it the discovery in the Elasmobranchs of a fourth branch of the trigeminal nerve, to have been termed the *palato-nasal* or *hyporhinal*. This term was intended to express the fact that, in relation to the trabeculæ, this branch of the fifth cranial nerve, together with the ophthalmic (for which he had already introduced the correlative term *orbito-nasal*, in his article "Amphibia," Encyclop. Brit., Vol. i. Edit. 9, p. 767), repeats the condition of the other cranial nerves in relation to their visceral arches and clefts, and thereby presupposes the existence of a præ-oral cleft. And, further, he was building up an argument on this basis to show that in these facts there lies the explanation of the mode and point of termination anteriorly of the notochord.—G. B. H.

² K  pffer, C. von: Stud. d. vergl. Entwick. Kopfes d. Kranioten, Hft. i. *Acipenser*: M  nchen, 1893, p. 89.

region to have been the first seat in order of time of the development of dermal plates¹.

Passing to the palate, it is seen that at this stage approximation is most marked in front, for while the vomers have met in the middle line, the pterygoids are widely divaricated behind. A noticeable feature is the fact that the palatines, which support the orbital floor, have apparently shared in the afore-mentioned rapidity of growth. From this stage onwards, the salient feature in progressive development is the closing in towards the middle line of the bones of both the cranial roof and palate, rendered possible by the fact that the most rapid phases in the growth of the brain have now passed. Comparison of Pl. III. figs. 11 & 12, and Pl. IV. figs. 5, 6, and 8, will render clear the changes undergone in the individual bones during the process, which it is not necessary to describe in words.

It is at the stage (R) that the parasphenoid first appears, in the form (Pl. III. fig. 12, *p.s.*; in section in Pl. IV. fig. 1) of a minute bony element which would most certainly be lost to sight in ordinary dissection, lying freely beneath the antero-median border of the post-pituitary plate. With advancing development it assumes an arrow-head shape and a more intimate relationship with the basis cranii, fusing by its broad posterior extremity at Stage S with the basisphenoids, and closing the pituitary foramen as it does so by extension anteriorly (Pl. IV. fig. 3).

We have already drawn attention (*anteà*, p. 2) to the interest attaching to this bone. It was overlooked by Günther, Brühl, and others, and its discovery was first claimed by Fritsch, who believed he had observed it as an independent element². Baur immediately challenged the alleged independence³, and gave an accurate account of its limitations in a young individual. Fritsch compared the supposed parasphenoid with that of *Hyloplezion*, and comparison of his figure of this with that given by Credner (*op. cit.* p. 513) of the presumed co-ossified basi- and præspenoids of *Palæohatteria* at once arouses suspicion by the close similarity in shape of the two; while further complication arises from the fact that Baur, commenting on Credner's discovery, regards⁴ his basi-præspenoid as a parasphenoid alone. Fritsch for *Sphenodon*, and Credner for *Palæohatteria*, were dealing with the compound basi- and parasphenoid, and were therefore in error. Baur was right only in his delimitation of the parasphenoid of *Sphenodon*.

The pterygoids, as already remarked, are developed widely apart, apposition in the middle line commencing anteriorly at Stage R, at which (Pl. III. fig. 12, *pg.*) they already reach the vomers—*i. e.*, their forward extension is thus recognizable as soon as

¹ Cf. Newberry, J. S.: Monogr. U.S. Geol. Survey, vol. xvi. 1889, p. 103, pl. xlv.; and Jæckel, O.: Sitzb. Ges. naturf. Fr. 1892, p. 90.

² Fritsch, A.: Fauna d. Gasköhle d. Permform. d. Böhmen, Bd. ii. 1889, p. 58.

Baur, G.: Zoolog. Anzeiger, Bd. xii. 1889, p. 45.

⁴ Baur, G.: Amer. Journ. Sci. 1889, p. 311.

the bones assume a mutual relationship, and is not brought about by ontogenetic growth. At Stage R (Pl. III. fig. 12) it will be observed that the anterior edge of the palatine (*pa.*) is transverse and that the vomers (*vo.*) lie wholly in front of them; whereas at Stage S (Pl. IV. fig. 6) the palatine border is angulated and the vomers are correspondingly modified. Proof that this change has arisen by backward elongation of the vomers, lies in the study of the relationships to the posterior nares, and it therefore follows that in the all-characteristic vomero-ptyergoid apposition the vomer has played a part. Boulenger, one of the advocates of the Rhynchocephalian affinities of the Chelonia, has called special attention¹ to a similar apposition in this order; but concerning it the process is the reverse of that of the adult Rhynchocephalian, it being the vomer which for the most part reaches back to the pterygoid. Judged by the foregoing ontogenetic changes undergone by the developing Sphenodon, this feature, instead of presenting, as might appear, a difficulty in the way of the acceptance of the said affinity, strengthens it, since both bones are in both groups of animals involved in the apposition, though in an inverse degree.

In Ichthyosaurus the vomers extend back divaricatingly behind the nares, and the pterygoids, inserting themselves between them, extend forwards between the nares². Taking the Stage R of Sphenodon as the starting point, the Ichthyosaur might well represent one extreme of modification, the Chelonian, through the adult Sphenodon, an opposite one; and in consideration of accepted views of the Chelonian affinities of the Plesiosauria³, it is interesting indeed to find that in these they are the vomers which longitudinally extend⁴.

The interest in the pterygoid of Sphenodon does not stop here, for, on examining its basicranial articulation we have found a synovial joint to be present and an independent interarticular cartilage (Pl. 4, figs. 1 & 3, *m.p.*), which flanks the inner face of the pterygoid and has an essential similarity to the meniscus mandibuli. We therefore propose to term it the *meniscus pterygoideus*⁵.

Cognate to the study of the pterygoid is the presence of a process of the squamosal hitherto unrecognized, which (Pl. IV. fig. 11, *sq.*¹) extends downwards and forwards between the quadrate and pterygoid, and, together with a process arising from the posterior border of the squamosal (*sq.*², Pl. IV. fig. 9 and Pl. V. fig. 13), embraces the expanded otic head of the quadrate. Both are present in the adult, the hinder process being the less conspicuous of the two.

¹ Boulenger, G. A.: Brit. Mus. Catal. *cit.* p. 17.

² Cf. Baur, G.: Anat. Anz. Bd. x. 1895, p. 458, fig. 1.

³ Cf. Andrews, C. W.: Quart. Journ. Geol. Soc. vol. lii. 1896, p. 251, fig. 2.

⁴ Cf. Andrews, C. W.: Geol. Mag. (iv.) vol. iii. 1896, p. 4, and Ann. & Mag. Nat. Hist. (6) vol. xv. 1896, p. 345.

⁵ Parker has undoubtedly seen and figured this in Zootoca (Phil. Trans. 1879, p. 612, & pl. 45, fig. 4), but his descriptive paragraph (§ 7) can hardly be said to adequately describe it.

The "Squamosal."—This bone has been most fully described by Baur, who¹ has accurately dealt with its relationships to the parietal, postorbital, jugal, quadrato-jugal, quadrate, and paroccipital process. It is unnecessary here to recapitulate the details of this association, which our figures render sufficiently clear, except to remark that we have extended the relationship to the pterygoid.

In the progress of investigation into the comparative osteology of the fossil reptiles, the varying conditions of the squamosal and supratemporal, one or both of which may be present, have become the subject of much consideration. The presence of the two has been regarded as a lowly characteristic, if only by way of analogy to the Stegocephalia. Cope and Baur are conspicuous among those who have utilized these bones in the determination and discussion of affinity, and nothing short of a deplorable confusion has arisen from their inconsistency in the usage of terms², and the fact that while one of them arrived at an inversion of the order adopted by certain contemporary writers, he finally complicated matters³ by needlessly reviving for the reptilian squamosal Owen's term "prosquamosal." A final agreement was never arrived at, and the question therefore arises as to which of the two bones is for the future to be regarded as the supra-temporal.

As a general rule these bones lie side by side in the same transverse plane. The term supra-temporal was applied by Bakker to the inner one⁴, in dealing with the fish skull. Cuvier denoted the presumably homologous bone in reptiles the "mastoid"⁵; and Owen, retaining this term, applied⁶ to the outer of the two (Cuvier's "temporal") the term squamosal. To be consistent, therefore, on the assumption that the inner of the two bones, having similar relationships in fishes and reptiles, is homologous, convenience and precision are met by terming the inner the supra-temporal, the outer the squamosal. And it is in this sense that we use these words⁷.

Our knowledge of the palaeontological history of the Rhynchocephalia has during recent years been materially advanced by the description by Lortet of remains from the Jurassic of France. In his memoir already cited (*antea*, p. 3) he drew attention in *Saphæosaurus* (*Sauranodon*) to a "parieto-squamosal" complex, in respect to which

¹ Baur, G.: *Anat. Anz.* Bd. x. 1895, p. 321.

² Cf. Baur, G.: *Anat. Anz.* Bd. i. 1886, p. 349, and Bd. ii. 1887, p. 657! and, as an awful example, the series of notes embodying the dispute between him and Cope in *Amer. Nat.* vols. xxix. & xxx.

³ Baur, G.: *Anat. Anz.* Bd. x. 1895, p. 320.

⁴ In Cuvier and Valenciennes, *Hist. Nat. des Poissons*, t. i. 1828, p. 338.

⁵ Cuvier, F.; *Ossements Fossiles*, t. x. 1836, p. 14.

⁶ Owen, R.: *Catal. Osteolog. Series R. Coll. Surgeons*, vol. i. 1853 (table), p. xxxviii.

⁷ Concerning the afore-mentioned confusion, Fraas for example, in his revisionary memoirs on the Ichthyosauria and Stegocephalia, following in respect to the latter the lead of Huxley, Miall, Fritsch, and Credner, refers to the inner bone as the squamosal, the outer as the supra-temporal. Zittel adopts the Huxleyean order for the Reptilia and Stegocephalia, with confusion arising out of the interpretation of the latter in the *Lacertilia* as the quadrato-jugal. Brühl is still more glaringly inconsistent and contradictory; while even

Boulenger first showed him¹ to be probably in error. Baur, accepting Boulenger's correction, has sought to show² that the bones regarded by him as the supra-temporal and squamosal lie within the area of the "squamosal" of Sphenodon, and that that bone is therefore compound. Shuffling the terms, he regarded the body of the latter with its laterally visible processes as a "prosquamosal" ("squamosal" *auct.*) and its posterior ascending process as the squamosal ("supra-temporal" *auct.*).

Seeking for evidence in support of this in the Tuatara, Baur admits that none was forthcoming in a skull of 25 mm. in length (*op. cit.* p. 321). Not only have we failed in all attempts to detect any such separation, but also to observe at any period traces of a second element. While we fully admit that this so-called "squamosal" of Sphenodon combines the structural relationships of the supra-temporal and squamosal as originally defined, failing the discovery of any trace of its supposed double nature, we are disposed, on consideration of the behaviour and all detailed relationships of the supra-temporal in the Lacertilia, to regard it as a squamosal, and to interpret its ascending limb, which meets the parotic process of the parietal, as secondarily acquired. The alternative would be the introduction of a new term, in which neither "squamosal" nor "temporal" were compounded, but we have no wish to render confusion more confounded. The future can only settle the question, and we are content to leave it to that.

The Quadrato-jugal.—This bone, as is well known, was first recognized in Sphenodon by Dollo³, and later more fully described by Baur⁴. We have nothing to add to their descriptive account of it. Its most characteristic feature is its enclosure with the quadrate (*qu.* & *q.j.*, Pl. IV. figs. 7 & 9) of a conspicuous foramen. Osawa, the latest writer upon it, terms it (98^a. pp. 499 & 520) the "tympanic," presumably on account of his inability to regard the mammalian tympanic as the homologue of the quadrate; and associated with the study of this bone there is a matter of no little importance, if, as we believe, the tendency of our time is in error.

Baur, in 1889, argued⁵ against the generally accepted belief that the single

Smith Woodward is not uniform in his terminology. Boulenger, on the other hand, is so, and, like ourselves, he retains the terms for the bones to which they were originally applied—*i. e.* for him, in both fishes and reptiles, the inner is the supra-temporal, the outer the squamosal. Difficulty admittedly arises when but one bone is present, and there is no doubt that in many such cases the problem can only be solved developmentally; but, on comparison of those lizards in which both bones are present, we believe him to be right in regarding the bone which alone suspends the quadrate in the Ophidia (Brit. Mus. Cat. "Ophidia") as the supra-temporal, and not the squamosal as do Huxley and his followers.

¹ Boulenger, G. A.: *Ann. & Mag. Nat. Hist.* (ser. 6) vol. xi. 1893, p. 209.

² Baur, G.: *Anat. Anz.* Bd. x. 1895, p. 322, *cf.* also *Amer. Nat.* vol. xxx. 1896, p. 145.

³ Dollo, L.: *Bull. Mus. R. Nat. Hist. Belg.* t. ii. 1883, p. 235.

⁴ Baur, G.: *Zool. Anz.* Bd. ix. 1886, p. 685.

⁵ Baur, G.: *Journ. of Morphol.* vol. iii. 1889, p. 473.

temporal arch of the Squamata represents only the upper arch of the Rhynchocephalia, basing his conclusions on the surmise that the quadrato-jugal is not unrepresented in the former as is usually supposed, but that the bone generally termed the "squamosal" is its homologue. Somewhat similar conclusions follow from the later determinations of Gaupp, laborious but unconvincing, in which he seeks to show¹ that the bone hitherto known as the quadrato-jugal in Batrachia and Birds must be for the future termed the "quadrato-maxillary," and that for the quadrato-jugal in Crocodilia, Chelonia, Rhynchocephalia, and Lacertilia, the term "paraquadrate" must be employed.

Baur assumes that the Squamata "never possessed an infra-temporal fossa, but that the broad arch was reduced from below in the same way as in the Testudinata" (*op. cit.* p. 473). It is beyond the scope of this memoir to fully discuss this question, voluminous in itself, but there tells strongly against the interpretation of the bone which in the "Squamata" reaches the head of the quadrate with that which in the Rhynchocephalia flanks its lower articular border, the fact, long ago pointed out by Huxley², that in the living Lacertilia there is present a ligament having the relationships of the latter. And, further, argument by analogy to the living Urodela, in which, while the maxillo-jugal arch is complete in bone only in the Eastern genus *Tylostotriton*³, a similar representation is present in ligament which may extend even into the maxillary region, places a further obstacle in the way of its acceptance. All recent investigation has gone to show that the Reptilia and the Batrachia are the diversely modified descendants of the Stegocephalia; and the fact that in them the supra-temporal, squamosal, and quadrato-jugal coexist in a transverse series tells with great force against this seductive argument.

The "Septo-maxillary."—This bone was originally described in *Sphenodon* by Osawa (98°. p. 503) as a small semicircular element attached by fibrous tissue to the vomer, and he therefore named it a "turbinal." In this he was unquestionably in error. The bone was figured and described by Parker in *Zootoca*⁴ as the septo-maxillary, and under this name it has been more recently described by Gaupp in other lacertilian embryos. Concerning its detailed relationship, he associates it with the support of the septum nasi internally and with that of the border of the cartilage enclosing Jacobson's organ superficially (*op. cit.* Ber. p. 10). The bone present in *Sphenodon* (Pl. IV. fig. 2, *s.m.x.*) is still more superficial in position and free of the nasal septum than this. In consideration of the fact that whereas here the Jacobson's organ is completely roofed in cartilage, in the lizard, according to Parker, the septo-maxillary fulfils that function⁵,

¹ Gaupp, G.: *Morphol. Arbeiten*, Jena, Bd. iv. 1895, p. 77.

² Huxley, T. H.: *Anat. of Vertebr.* 1871, p. 190.

³ Riese, H.: *Zoolog. Jahrb., Anat. Abth.* Bd. v. 1892, p. 99.

⁴ Parker, W. K.: *Phil. Trans.* 1879, pt. ii. p. 609.

⁵ Parker, W. K.: *Phil. Trans.* 1879, pl. 44. fig. 5.

we are disposed to regard the bone as its homologue. It is figured in the macerated state at Pl. VI. fig. 1, *s.m.x.*, and, as remarked by Gaupp, is a membrane-bone.

The supposed "lachrymal" of Günther (67. p. 597), accepted by Hofmann¹, Seeley (?)², and Credner³, has no existence.

The Præ- and Postfrontal and Postorbital.—The two former are proved by their development to be membrane-bones⁴, and examination of Pl. IV. fig. 10 shows that they are neither of them compound and that there are no correlated chondro-cranial ossifications.

The postorbital has the customay relationships of that bone and is very large⁵.

¹ Hofmann, C. K.: Bronn's Klass. u. Ordng. d. Thier-Reichs, Bd. vi. Abth. 3, pl. 66. fig. 5.

² Seeley, H. G.: Journ. Linn. Soc., Zool. vol. xii. 1876, p. 184. "In front is a small lachrymal, which is not found in Chelonians." The context is not clear.

³ Credner, H.: *op. cit.* p. 510. Baur has pointed out the error here, Amer. Journ. Sci. vol. xxxvii. 1889, p. 311.

⁴ We retain the term *præfrontal*, as one now in general use. It is, however, unfortunate (since it was originally applied by St.-Hilaire, in 1807, to a cartilage-bone, which Cuvier in his 'Leçons' defined as transmitting the olfactory nerve) that it should have become applied indifferently to various cartilage and membrane bones occurring in the *præfrontal* region. A great confusion exists with respect to the modern usage of the term, but it does not materially affect our work.

⁵ The study of the postorbital in *Sphenodon* is intimately bound up with Günther's work upon the living *Crocodylia*, which possess but a single so-called "postfrontal." On the basis of comparison with this he came to regard the postorbital of *Sphenodon* (which, following Stannius, he termed "quadrato-jugal") as "a detached portion of the postfrontal" (67. p. 598). Baur discovered in 1886 (*Zool. Anz.* Bd. ix. p. 740) that both postfrontal and postorbital are present in *Belodon*, and accepted Günther's conclusion concerning *Sphenodon*. Their reasoning suggests an origin of the postorbital from the postfrontal, rather than that both bones were originally distinct, and that the presence of one or both is due to variation by co-ossification with age. And, as bearing upon this, we submit the following observation:—Cuvier showed that in the *Iguana* ('Leçons,' t. x. p. 14) there are two bones occupying the region of the postfrontal of other Lizards. He applied to both this term, and figured them as attached side by side to the postorbital process of the frontal. In our own example the hinder bone alone has this relationship, the former being pushed forwards in front of the process named. Comparison with the single "postfrontal" bone present in many Lizards—*e.g.*, the familiar backwardly-pointed bone of *Varanus*—shows this to have the detailed relationships of Cuvier's two "postfrontals" in *Iguana*, wherefore suspicion arises that it is perhaps compound. That this may be the case is proved by the skull of a young *Tupinambis* in our possession, in which, as Mr. M. F. Woodward has shown us, two bones are present in its place. Contrary to what happens in *Iguana*, the postfrontal is alone attached to the frontal and the postorbital to it. This notwithstanding, it follows that the bones described by Cuvier in *Iguana* are the postfrontal and postorbital, and that they are both represented in the varanoid type (*cf.* also Gaupp on the embryo *Lacerta*, in *Morph. Arbeiten*, Bd. iv. p. 77, pl. vi. fig. 9). We are also indebted to Mr. Woodward for drawing our attention to a skull of the Green Turtle (*Chelone mydas*) in our Teaching Collection, in which that portion of the "postorbital" naturally connected with the anterior two-thirds of the frontal is on the left side distinct—*i. e.*, an independent postfrontal is present.

These facts go far to prove that in the *Reptilia* generally, where either a single "postfrontal" or "postorbital" is alone present, it may be a compound of these two; and they certainly suggest that the postfrontal of the living *Crocodylia* may have gone elsewhere than over to the frontal, as surmised by Baur.

The Mandible.—The mandibular ramus has been shown by Baur to consist (95^a, p. 413) of the six elements usually present in that of other Reptilia. He originally described it in 1891¹ as resembling most closely that of those Chelonians in which the angular and supra-angular, apposed behind the splenial, under-arch the articular, and as destitute of the 7th element or “præsplenial” described by him in these animals. We have only to add that at the latest stage observed by us (T) the articular has not yet appeared, the articular region being still cartilaginous, and that at Stage S the angular and supra-angular (*s.a.*, Pl. IV. fig. 4) are still separated by the splenial (*sp.*).

6. THE APPENDICULAR SKELETON.

The Pectoral Girdle.—Concerning this we have little to record. The simplicity of the coracoid was pointed out by Günther, in the remark (67. p. 611) that it has “no notch whatever.” Fürbringer, in a passing allusion seven years later², commented on the rounded border and feebly ossified state of this (Pl. VI. fig. 6, *cor.*), and there can be no doubt that in respect to these features it simplifies the Lacertilian type. As pointed out by Fürbringer, however, the Chamæleons approximate to a similar condition, but it may be questioned whether the “simplification” in them is not due to secondary causes. Ossification takes place during Stages S and T, on lines common to both the Batrachia and Reptilia. An interesting detail is the early appearance of the clavicle, viz. at Stage Q (Pl. VI. fig. 4, *cl.*), at which no cartilage-bones are anywhere present in the axial skeleton. The interclavicle appears later. We have failed in all attempts to find evidence of a cartilaginous predecessor of these bones.

The relationships to the sternum we have already described (*antea*, p. 33).

The Pelvic Girdle.—Günther accurately described the adult girdle, except that he applies to the ileo-pectineal process the term “uncinate” (67. p. 615). Like the shoulder-girdle, it is at Stage Q fully chondrified. Its two halves (Pl. VI. fig. 7) are united, and there is a considerable cartilaginous symphysis (*c.i.p.*) which in the mid-ventral line separates the cordiform fenestræ (*f.c.*). With later growth (at Stage R) a backwardly-directed median process (the hypischium of Mehnert³) becomes conspicuous, but it is never segmented off or ossified to form an “os cloacæ” as in *Lacerta*. The epipubic cartilage (*e.*) like it is simple—*i. e.*, there is nothing to suggest those processes of bifurcation and subdivision recorded for certain *Lacertilia*.

Interest attaches to the ligamentum medianum pelvis, from the fact that while Wiedersheim has described⁴ in its place in the adult a cartilaginous tract uninter-

¹ In his 1895 notes he admits a transposition in those of 1891 of the terms angular and splenial, but it does not affect his comparison.

² Fürbringer, M.: *Morph. Jahrb.* Bd. i. 1876, p. 643.

³ Mehnert, E.: *Morph. Jahrb.* Bd. xvii. 1891, p. 123.

⁴ Wiedersheim, R.: *Zeitschr. wiss. Zool.* Bd. liii. 1892, p. 54.

ruptedly continuous with the epipubis and hypischium, Mehnert has denied (*op. cit.* p. 142) a "skeleto-vicarious" significance to this ligament for *Lacerta*. Our developmental material shows that Wiedersheim was in error, since the ligament is already present (Pl. VI. fig. 8, *li.p.*) at Stage R. Concerning Mehnert's conclusion, we can only add that in *Sphenodon* the ligament is preformed in cartilage (Pl. VI. fig. 7, *ci.p.*) at first of considerable extent, and that with advancing development, correlatively with the expansion of the pelvis and widening of the cordiform fenestræ, this undergoes a relative reduction with accompanying replacement in fibrous tissue. If Mehnert is correct, the cartilaginous symphysis and the primarily small size of the fenestræ carry *Sphenodon* so much nearer the Batrachia.

In the course of our work our attention became arrested by the fact that there are apparently two types of hip-girdle represented in the adult. We append camera-lucida figures of these. When viewed from beneath, it is evident that the essential difference

Fig. 13.

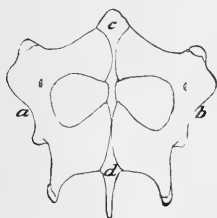
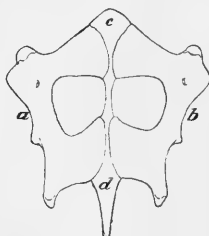


Fig. 14.



Camera-lucida outline sketches of extreme types of the adult pelvis of *Sphenodon*.

13, least expanded; 14, most expanded. Nat. size.

between them is one of increased length as compared with breadth. In the pelvis of the least expanded type (text-fig. 13) the cordiform fenestræ are more rounded than in the most expanded, in which they appear (fig. 14) angular; and we find that whereas in the least expanded type the transverse measurement across *a-b* is about equal to that along *c-d* (fig. 13), in the most expanded (fig. 14) *c-d* is greater. We note, however, that in all cases the distance between the opposite limits of the cordiform fenestræ is equal to that of the symphysis ischii from the vertebral column and to the transverse diameter of the sacrum.

For want of material undoubtedly mature upon which to base further comparison, we are unable to decide how far this is or is not a sexual matter; but we are disposed to believe the contrary. The only other case known to us, which is at all analogous, is that of the presence of two still more distinct types of scapulæ in an extensive collection of bones of the Australian Dugong brought home by Professor Haddon. F.R.S., from Torres Straits in 1889, now in the custody of one of us.

The Long Bones.—Under this head we include the humerus and femur, radius and tibia, ulna and fibula. They have all been so often described, from Günther to Osawa, that detailed recognition by us would be superfluous. We would only add that the condylar foramina of the humerus, originally observed by Dollo (84), are both fully formed at Stage Q (Pl. VI. fig. 10, *f.en., f.ec.*), and that the inner has from the first period of differentiation its canal-like character.

The long bones are the first of all the cartilage-bones to ossify.

Carpus and Tarsus, with Phalanges.

It is evident, from the study of both carpus and tarsus, that chondrification sets in correspondingly (for the tarsus, *cf.* Pl. VI. fig. 15). One inexplicable feature is the long duration of the cartilaginous state of both. Ossification begins in both post-axially (as is seen in fig. 14 for the carpus), but not until the rest of the limb is fully ossified.

We have examined both carpus and tarsus at all stages of development back to Q, where these elements are first chondrified. To make sure of detail, we have employed, beyond clarified dissections, serial sections cut horizontally.

The Carpus.—Günther described ten carpal elements, and in this he has been followed by others. He appears to have missed one of the centralia, and to have confused the other with the proximal elements, which he describes as five in number (67. p. 612). Osawa, the latest writer on the subject, correctly records eleven elements (98^a. p. 528), the eleventh being the second centrale, detected by Bayer (84. p. 237), who first applied to the parts a rational terminology. It was, however, independently discovered by Dollo and Baur (86^a. p. 188), the latter opposing Bayer's conclusion that its supposed absence is due either to disappearance or union with another carpal element. In this he was right, for we find it always present.

None of the afore-mentioned observers describe the precise size and relationships of the two centralia to each other and the adjacent carpal elements. Osawa, however, gives a very different delineation to the dorsal and ventral aspects of the same pair, and figures the præaxial as outwardly extended between the radiale and first carpale as seen from the dorsal surface (98^a. p. 527, figs. 13 & 14). While we can confirm the accuracy of this, we are able to record further suggestive details. From a comparison of our figs. 12 and 13 (Pl. VI.) which represent the opposite carpaes of the same individual, we find that the right (fig. 12) is normal but that the left (fig. 13) is exceptional, in the fact that the præaxial centrale (*pr.c.*) is smaller than the postaxial (*po.c.*) and lies wholly between the radiale and the first carpale, instead of merely extending between them. The postaxial centrale, on the other hand, is correspondingly enlarged, whereby it articulates with the second carpale, as well as with the third and fourth, to which alone it is usually related. There is thus to be observed an inverse

proportion to that of the corresponding centralia of the other limb (fig. 12). Bayer has suggested that in the presence of the double centrale *Sphenodon* exhibits a Batrachian tendency, drawing attention to the great extent to which the living Urodela are doubly centralial. One of us has, with another, attempted to show¹ that the presence of a second centrale carpi is a diagnostic character of the Anura, and this goes to support Bayer's argument. As to centralia, however, Wiedersheim has demonstrated² the presence of three in the Axolotl; and with these facts in mind it occurred to us that the inequality in development of the two centralia in *Sphenodon* might possibly be due to the presence of a third, which had fused with the opposite fellow on the opposite sides in the pair of limbs under discussion. At Stage Q the condition of the centralia was found to be the same as in the normal adult; but in a young specimen belonging to the R. College of Science, Dublin, the præaxial centrale is on each side ossified from two independent centres (Pl. VI. fig. 14, *pr.c.*), and in such a form that while co-ossification of them would bring about the condition of the right limb (fig. 12), co-ossification of the middle nucleus with the postaxial centrale (*po.c.*) would result in that of the left.

Bruhl, for some unaccountable reason, systematically terms³ the pisiform of Reptiles the "ulnar sesamoid"! Concerning the rest of the proximal carpals and the centralia we have nothing to add.

The distal carpals, stated by Günther to be five in number, are by Bayer enumerated as four. As he was dealing with a young animal he found only the 4th carpal ossified. This is seen to be the case on the left side of our figs. 12 and 13, in which (Stage T) the rest of the carpus is still cartilaginous (*cf.* previous statement on p. 60). Bayer believed that the 5th carpal is to be sought in the cartilaginous head of the related metacarpal (*op. cit.* p. 241); but in this he was mistaken, as pointed out by Baur in that it is always present and distinct, though small (Pl. VI. figs. 11 to 14).

We have no variations or other matters to record concerning the phalanges of the fore limb.

The Tarsus.—Günther describes two proximal and two distal elements, and is doubtful about a fifth—the fifth tarsal. He alludes without name to the "meniscus" of Born, which we figure (Pl. VI. fig. 18, *mn.*). Osawa describes one proximal element, the "proximal tarsale," and four distal—five in all. He regards the meniscus (p. 504) as the first tarsale, while Born associates it in the *Lacertilia*⁴ with the centrale. Both are in error, for whereas the meniscus does not appear till Stage S (when all the tarsal elements have been formed), the first tarsal arises at Q (fig. 16) as a separate element (I.), and at Stage R, when fully chondrified, unites with its metatarsal. The meniscus is thus proved to be an accessory element (*cf.* Born, *Morph. Jahrb. Bd. vi.* 1880, p. 67).

¹ Howes & Ridewood: P. Z. S. 1888, p. 177.

² Wiedersheim, R.: *Morph. Jahrb. Bd. vi.* 1880, p. 581.

³ Brühl, C. B.: *Zootomie aller Thier Kl.*, Wien 1880, pls. 31-34 and 53 & 54.

⁴ Born, G.: *Morph. Jahrb. Bd. ii.* 1876, p. 25.

Born, as is well known, gave it as characteristic of the Lacertilia that tarsalia I and 2 were probably united with the corresponding metatarsals; and in this he has been followed by Bayer (p. 243), who claims a phylogenetic union for these! Osawa rightly figures the second tarsale of *Sphenodon* as distinct; and we find that from Stage Q (fig. 15) to the adult state this is present as an independent element (as in fig. 18) which becomes extensively ossified.

Perrin asserts (95. pp. 44 & 97) that five separate distal tarsalia are present, and his figure 9 may illustrate but does not adorn his text! We are at a loss to understand what he has figured; but one thing certain is that in ascribing three phalanges to the fifth digit he is in agreement with Bayer, who is inclined to regard the hooked bone, which by its angulated head articulates with the outer face of the fourth tarsale, as the fifth of that series. As a salient objection to regarding this as a metatarsal he seeks to show that on the Güntherian determination *Sphenodon* would be an exception to the rule among Lizards in possessing more than three phalanges to the fifth digit; but it does not occur to him that this statement is tantamount to admitting that the angulated bone is in most Lizards a metatarsal, and that it thereby nullifies his argument. Dismissing for the moment the facts of development, the discovery by us that a specimen preserved in the R. College of Surgeons Museum is possessed of three phalanges on the outermost digit of one hind limb, and four on the other, dispenses with the necessity for further discussion of this point, except to remark that among the *Chelonina*, *Pleurodira* (*Emydura*) for example, we meet with a quadriphalangeate fifth toe. The matter is clearly one lying within the range of individual variation.

Developmentally, this bone, angulated from the first period of its differentiation (Stage Q, Pl. VI. fig. 16, v.), ossifies at R (Pl. VI. fig. 17), at the same time and in the same manner as the other metatarsals; and we have already pointed out that the tarsal elements do not ossify until T, when the metatarsals are formed. And were further proof needed of its metatarsal homology, it is forthcoming in the totally different manner of ossification of the carpus and tarsus and the metacarpals, metatarsals, and phalanges—the former ossifying endosteally, the latter ectosteally.

There is no trace in *Sphenodon* of tarsale 5 actual or potential, and no evidence developmentally for the belief of Baur that it is incorporated in the fourth tarsale (*Zool. Anz.* Bd. ix. p. 189)¹. It seems to have vanished even from the ontogenetic record.

Concerning the proximal tarsal series, Osawa describes one confluent element; and Günther evidently had to deal with a specimen in which they were just uniting, for the "suture" to which he refers as "scarcely visible" is recognizable, as in our Pl. VI.

¹ We are disposed to believe, with Forsyth Major (*Trans. Linn. Soc., Zool.* vol. vii. 1899, p. 510), that the compound nature of the "cuboid" is seriously open to doubt.

fig. 18, in all but old individuals. Bayer, finding the præaxial moiety of the "astragalus" cartilaginous, regarded it as the tibiale, and the whole "astragalus" as consisting of the centrale¹ and the intermedium, the "calcaneum" being to him the fibulare (*op. cit.* p. 243). Perrin, going further, names the "astragalus" (*op. cit.* p. 44) the "tibio-centro-intermediare."

Development at Stage Q shows (Pl. VI. fig. 16) that at the chondrification period the "astragalus" and "calcaneum" are independently chondrified, and a feeble ypsiloid differentiation (accurately indicated in the fig.) may be observed at what would be the apposition lines of the tibiale (*t.*), centrale (*tc.*), and intermediare (*i.*), were they distinct. In an earlier embryo of the same stage (fig. 15) we found the intermediare (*i.*) and fibulare (*f.*) chondrified and separated by a foramen apparently homologous with that known as the f. arteria perforans mesopodii (*fb.*), the centrale (*tc.*) and tibiale (*t.*) being procartilaginous, although in close apposition with the intermediare and with each other. Bayer and Perrin had correctly surmised!

7. THE DENTITION.

The detailed study of the tooth-genesis does not fall within the scope of our work, but we have one or two interesting anatomical facts to record.

Firstly, as to the vomerine teeth. No trace of them in a calcified form is forthcoming up to Stage T, the oldest we have examined. We can add nothing to what is recorded in the latest account given by Siebenrock². It may be that we have not happened to deal with embryos in which they were developing, or, perhaps, that these clearly vestigial organs attain their full development late.

Baur would seem to be wrong in the surmise (96^b. p. 437) that they exist in young specimens and disappear in old age³.

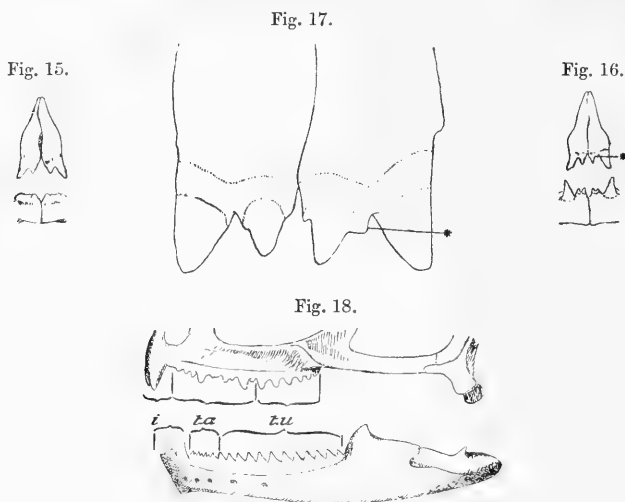
The Incisors.—These have been correctly shown by Dendy (99^a. p. 77) to be represented in the young stage by three pairs of "distinct pointed conical teeth" above and below, and not by two as believed by Günther (67. p. 602) and Baur (p. 436). It is worth remarking, however, that Knox had already recorded the supposed existence of three pairs in the upper jaw (69. p. 18), and Newman in the lower (77. p. 234), the former stating that they were confluent at their bases. This is the case at our Stage T

¹ Baur's passing remark (Zool. Anz. Bd. ix. p. 189) that he found this represented by a piece of cartilage which was "eingeklebt" is suggestive of begging the question.

² Siebenrock, F.: Transl. cit. p. 309.

³ Further search is necessary to ascertain how far the vomerine teeth are or are not represented during ontogeny, and a former pupil of mine, Mr. H. Spencer Harrison, has undertaken to immediately work out this and other problems connected with the dentition of *Sphenodon* as the subject of a special communication to appear in the Qu. Journ. Microscop. Science.—G. B. H.

(Pl. II. fig. 15), the outer tooth of each set being somewhat the larger of the three. At Stage S (fig. 14) all are seen to be free, and the outer still large. Beyond the mere inference of fusion, Dendy does not state the method by which he presumes these pointed incisors to be converted into the tusks of the adult. As a rule each of the upper tusks, when fully formed, is doubly pointed (or, as remarked by Günther, "notched") (*cf.* text-fig. 15), there being a smaller internal cone, and a larger external one somewhat backwardly curved (text-fig. 16). In the lower jaw there are three cones (text-fig. 16), a larger external and two smaller internal, the three teeth which are



Illustrations of the dentition of *Sphenodon*.

Fig. 15. Incisors, front aspect, old individual. Fig. 16. The same, younger individual, little worn. Both nat. size. Fig. 17. Enlarged sketch of upper incisors of fig. 16, $\times 6$. Fig. 18. Complete adult dentition: nat. size. *i*, incisors; *l.a.*, cheek-teeth, alternating series; *t.u.*, cheek-teeth, structurally uniform series.

present having united with the mandible. That portion of the dentary element which bears them becomes, with them, clothed in an enamel-like substance, which justifies Günther's remark (67. p. 602) that the alveolar edge of the mandible is polished. Tomes¹ regards this substance as true bone.

In the embryonic upper jaw the middle incisor present early ceases to elongate (*cf.* Pl. II. fig. 15, *t.m.*) and at Stage T it becomes loose. The reason of this is evident from the fact that longitudinal section (Pl. II. fig. 16) shows it to be confluent

¹ Tomes, C.: Dental Anatomy, ed. 4, 1894, p. 253.

only externally with the premaxilla (*p.x.*) and not by its whole base, as is the case with the other teeth. We suspect that this tooth is early shed, but unfortunately our material does not embrace a specimen proving the point.

A possible source of error must not be here overlooked, in the fact that in the adult there may be present a small pointed cusp (text-fig. 16, *) between the two upper incisors, which at first suggests a persistent middle tooth. When, however, a tooth thus constituted is examined under a lens, it is found that the minute cusp has a counterpart (text-fig. 17) on the inner face of the inner tooth, and that, like this, it is but the product of its base. And since the teeth, when first formed, are simple cones, these lesser cusps must be due to secondary complication.

The palatal and maxillary teeth vary very greatly in appearance at different stages in development and periods of life. One conspicuous feature which has not been recorded is that at Stage S the maxillary teeth number 11 and the palatal 4-5 (*cf.* Pl. IV. figs. 4-6). These first-formed cheek-teeth usually alternate, a larger and a smaller occurring in succession, and not infrequently they may be arranged in recurring sets of three, a larger and two smaller to each. At Stage T the same numerical condition obtains (allowing for individual variation, most marked for the palatine teeth), but under the growth-processes at work the larger teeth have now increased in size. From this period onwards the numerical increase in the teeth as a whole is due to superaddition from behind forwards, and most of the teeth thus formed (*t.u.*, text-fig. 18) are uniform in size. Numerically they average about 6 on either side, and for the palate about 4-5, giving a total number of about 16-17 maxillary teeth and 9-11 palatal¹.

Passing to the mandibular series, we note an essential similarity to the maxillary, in the arrangement of the teeth first formed. At Stage S (Pl. IV. fig. 4) there are 11 alternating teeth as in the maxilla², but no others. On the assumption of Stage T the teeth of the alternating series, unlike those of the upper jaw, apparently cease to grow. Wear and tear supervening, and the development of the structurally uniform teeth continuing apace, these (*t.u.*, text-fig. 18) become predominant; and hence the condition herein delineated, which is of short duration, as the teeth of the alternating series (*t.a.*), now insignificant, become rapidly worn down.

Baur has described (95^b. p. 436) a *Sphenodon* skull, 25 min. in length, having two

¹ The number of teeth recorded by different observers ranges for the maxillary from 6 (Knox) to 17 (Colenso), and for the palatal from 5 (Knox) to 13 (Newman); for the mandibular from 13 (Colenso) to 19 (Günther). In the absence of detailed description and knowledge of degree of wear and tear, it is not possible to make use of these figures.

² This alternation is a striking feature. Among the Monitors it is often the case that in the fresh state the cheek-teeth are similarly, though more markedly, alternate, the elongated teeth being fixed to the jaws alternately with small ones which are freely displaceable at their bases. Can it be that there is a common determining cause at work here?

upper incisors and an eminence which he surmised suggested a third, and he remarked ¹ that each of the inner incisors on either side had a very small successional tooth, which he believed was never further developed. On examination of a series of sections of a 19 mm. example we find a similar tooth (Pl. II. fig. 16, *td.*) but behind the middle tooth of the three that are present (*tm.*). Baur's specimen appears to have suffered the loss of the middle incisor, and to justify our conclusion that this is shed. And while we are not sure whether our successional incisor is the same as his, or whether he and we were dealing with members of a series which may be formed, his conclusion that the tooth is never functional receives support from what we have observed ².

In describing the cheek-teeth, Baur attributed to the fifth maxillary and the first mandibular a successional tooth. This we have not been able to confirm. Passing to the structurally uniform series (*tu.*), we find these to mostly arise lineally. Pl. II. fig. 17, in its outlined portion, is a reconstructional drawing from horizontal microscopic sections at this period. The teeth drawn in outline (*tf.*) are fused to the maxilla and palatine, as indicated. Those drawn in colour, together with the shaded portion of the drawing, are from individual sections, the teeth which appear to represent the structurally uniform series (coloured yellow) being delineated in the position in which they arise.

The teeth of the adult *Sphenodon* have been defined by Günther (67. p. 601) as "acrodont in the strictest meaning of the term." Boulenger (Brit. Mus. Cat. cit. p. 1) regards them as "not implanted in alveoli"; while Tomes, ignoring the incisors, has written of the post-incisors that they are "acrodont," and he further suggests that the glistening investment of the alveolar edges, which Günther originally described and showed to "perform the functions of teeth when these are ground down in advanced age," is true bone. Baur refers (p. 437) to "alveoli" in his 25 mm. specimens, but gives insufficient details.

If we may infer from the foregoing that Tomes, ignoring the incisors, was suspicious of their being in the adult non-acrodont, we have to confirm his doubts. Thanks to Mr. M. F. Woodward, we have been enabled to examine a series of microscopic sections of both upper and lower incisors of the adult *in situ*; and concerning the upper there is evidence of surrounding bone—not as the result of a truly thecodont condition, but of an apparent secondary overgrowth subsequent to the union between tooth and jaw. Examination of Pl. II. fig. 18 shows in the case of a mandibular tooth that the truly acrodont condition is assumed at Stage S; and at Stage T the incisors show in our sections a condition intermediate between this and that above described. Further investigation of this topic is beyond the limits of our pledge to Professor Dendy, but, pending detailed study of the tooth-genesis, we would distinguish the condition occurring in at least the incisors as *hyperacrodont*.

¹ As usual, he writes (line 8) "innere" for "aussere."

² We have no material to show whether the embryo teeth which we herein describe do or do not become later replaced.

8. SUMMARY AND CONCLUSIONS.

Summary.—The following is a summary of the more important conclusions embodied in Sections 5 to 7 of the present Memoir:—

1. That two kinds of intercentra are formed: primary intercentra, originally paired and mostly preformed in cartilage; and secondary intercentra, which replace those throughout certain regions of the body, and are mostly median and arise by direct ossification outside the vertebral column.

2. That the primary intercentra persist in the caudal region to form the chevrons, and anteriorly for the first few segments, and that the secondary intercentra coexist with them in the anterior caudal region alone.

3. That the hyaline cartilages which go to form the vertebral centra are paired in origin.

4. That an intravertebral chordal plate is formed by transformation of the substance of the chorda within each vertebral centrum, and that the plate is continuous with the chordal epithelium, which becomes converted into a tunica lying inside the chordal sheath.

5. That during the final differentiation of the vertebræ the chorda becomes metamERICALLY segmented, and that there appears in each segment a central chordal vesicle at the point of greatest flexibility.

6. That in that part of the caudal region modified for "splitting" there are formed, by similar differentiation to that which gives rise to the intravertebral chordal plates, a series of intervertebral plates, and that the intravertebral plates play an important part in the casting of the tail, and may be possibly the seat of regenerative activity in the formation of the renewed caudal axis.

7. That the ribs arise in procartilage, in relation to the primary intercentra, with which they are the first differentiated skeletal elements; and that they are differentiated obliquely, the capitular portions in direct relationship with the intervertebral regions and the intercentra—the tubercular with the areas of differentiation of the vertebral centra and arches of the vertebræ behind. That these relationships are lost during later development for all but the third and fourth præsternal segments.

8. That the uncinates are separate in origin, with the possible exception of those of the penultimate and antepenultimate præsternal ribs.

9. That the cartilaginous brain-case is a product of the union of distinct ethmo- and orbito-sphenoidal plates, and that its bars and fenestræ are all attributable to direct processes of growth—*i. e.*, that it is not a fenestrated cranium of the cartilaginous fish type.

10. That the hypoglossus nerve-bearing region bears five pairs of nerves with four pairs of foramina, and that during development these become reduced to two each.

11. That the trabeculæ cranii play no part in the direct formation of the lateral cranial wall, and that they represent a pair of præoral visceral arches.

12. That the epipterygoid bone is the product of ossification of the ascending process of the pterygo-quadrate cartilage, and that the special feature of the quadrate bone is an extension of its ossific head into the latter for approximation to the epipterygoid.

13. That the columella auris and stapedial processes are alike direct derivatives of the hyoid arch, with which they are continuous at all stages, and that structural complication is due to overgrowth of the same.

14. That the upper end of the hyoid cornu is attached to the quadrate only, and that there is a fleeting "jointing" of the former throughout its course.

15. That in the meeting of the pterygoids and vomers, the latter play a part leading up to the conditions occurring in the Chelonia and Plesiosaurs.

16. The cartilaginous pterygo-quadrate is in its detailed characters most nearly comparable to that of the Apodal Batrachian Ichthyophis.

17. That each of the three segments of each of the "abdominal ribs" (gastralia) arises by union of a number of calcifications, and that the median segment may be paired. That the "plastron" is present in a degenerating form.

18. That in their early differentiation the membrane-bones of the head and face are predominantly circumorbital in position.

19. That there is no supratemporal bone recognizable at any stage as a distinct element.

20. That the hip-girdle in its development is of a lower type than the Lacertilian, and that there are two types of pelvis present in adults.

21. That the fifth tarsale has no existence in ontogeny, and that the basal element of the fifth digit of the hind limb is a metatarsal.

22. That there are apparently three centralia carpi represented during development, and that a centrale is incorporated in the "astragalus."

23. That calcified vomerine teeth are not present during encapsulation within the egg-shell.

24. That of the three pairs of upper incisors, the middle certainly disappear and the inner may become tricuspid.

25. That the cheek-teeth appear to consist of two series—an early developed alternating set, and a later posterior and structurally uniform set.

16. That there arise within the occipital region and the individual vertebral segments sustentacular ligaments, for support of the medulla and spinal cord.

Conclusions.—Paragraphs 16, 17, 20, and 22 of our Summary add fresh testimony to the belief in the Batrachian affinities of the living Sphenodon, while paragraph 15 strengthens the demonstration of its Chelonian resemblances and extends these to the Plesiosaurs. Paragraph 17 proves the creature to be a highly modified representative of its Suborder, but at the same time to pass through a developmental phase realistic of the lower Suborder of the Rhynchocephalia, as now classified; and the same is true of paragraph 24, by comparison with the Proterosaurs (especially Palæohatteria). Of the supposed Agamid affinities we have written enough (*antea*, pp. 4, 22, 46).

Sphenodon, judged from our standpoint, must be regarded as the surviving representative of that group of animals ancestral to all the living Sauropsida, and to at least the Dinosauria, Pterodactyla, and Ichthyosauria, of the past—if not of the Mosasauria and Dolichosauria also, and unquestionably intimately related to the Anomodontia. As concerning the unmistakable Stegocephalian affinities of the Rhynchocephalia, it becomes necessary to enquire more closely than hitherto into the sum of those characters which constitute a Batrachian a Batrachian—a Rhynchocephalian a Reptile.

Attention was in 1892 called by one of us (Journ. Anat. & Phys. vol. xxvi. p. 402) to the fact that whereas no Batrachian living or extinct was then known to possess more than two phalanges on each of its two innermost digits—the formula for the Class being 2 2 3 4 2, that of the Sauropsida being 2 3 4 5 4 (or something minus that by reduction), it would seem impossible to derive the Sauropsidan condition from that of any known Batrachian, not excluding the Stegocephalia. Recent investigation, however, has modified this aspect of the question. Firstly, there has been discovered an undoubted Stegocephalian ally having on the second digit of its fore limb three phalanges and on the third four, and for its hind limb the formula 2 3 4 4 3¹. And, again, in Credner's *Sclerocephalus* of the Permian, which, its massive quadrate notwithstanding, he places among the Stegocephalia², there existed a combination of the lowest Stegocephalian type, amounting, in the structure of its dermal skeleton, almost to the "Ganoidan," with a limb-skeleton (if the remains are rightly associated) of a veritable lizard—the phalangeal formula being 2 3 4 5 4 for the hind limb, and that clawed³.

Again, as to the sternum, it has also been pointed out by one of us ('Nature,' vol. xlviii. p. 269, 1891) that a sharp distinction may be drawn between the *coraco-sternum* of the Batrachia (*an archisternum*) and the *costal sternum* of the Amniota (*a neosternum*), the existence of which in any Batrachian or Stegocephalian has not been proved.

And as to the skull, the now well-known fact that whereas in the Amniota the hypoglossal nerve-bearing region, truncal in origin, is incorporated in the occiput, in the Batrachia these nerves are postoccipital⁴, once again opens the gap between the Batrachia and Amniota—indeed, so markedly, that our ideas may be systematized by

¹ Ceraterpeton galvani, A. S. Woodward, Geol. Mag. (dec. 4), vol. iv. p. 297 (1897).

² Credner, H.: Zeitschr. deutsch. geolog. Gesellsch. Bd. xiv. 1893, p. 639.

³ We are at a loss to understand the reason for the intercalation in the restored portions of the skeleton of *Pariasauros* in the British Museum of Natural History of a fourth phalanx to the second digit of the hind-limb, especially as in the original description of the specimen it is the front-limb of which it is said (Phil. Trans. vol. 183, B. p. 363) to be possible that one digit may have had four! We fail to discover evidence of more than three phalanges for any digit that is preserved.

⁴ Restricting the terms to the Terrestrial Vertebrata, we leave aside the question how far the vagus-bearing portion of the skull may be truncal also, and that of the undoubted parallelism which exists between the Amniota and certain Ichthyopsida, concerning the union of skull and vertebral column (*cf.* the masterly Memoir by Fürbringer, M.: Gegenbaurs Festschrift, Leipzig, 1897).

applying to the former condition the term *Archieraniate*¹, and to the latter that of the *Syncraniate*.

The characters of the occipital condyle and the presence of one, two, or, for the matter of that, of three condyles, no longer have the significance once attached to them as criteria of affinity.

Judged from this point of view, the Rhynchocephalia may well be regarded as a lowly group, ancestral to the Sauropsida as ordinarily defined, and intimately related to the Anomodontia; and while the latter, perhaps with or through the Pelycosauria of Cope, on the one hand gave rise to the Mammalia, they were probably with the Rhynchocephalia derived by diversity of modification from some common ancestral stock which carries us towards a group which must have been either Batrachian Reptiles or Reptilian Batrachians, as compared with forms extant—*i. e.*, they either possessed a coraco-sternum and an archieranium, or a costal-sternum and a syncranium, structural combinations which go hand in hand. If they were of the latter type, the living Batrachia must have suffered the loss of a costal-sternum and not a few of their distinctive characters must be indicative of retrogression. The argument applies equally to the quadrate and whether its representative in the living Batrachia is or is not vestigial, and, as concerning the parasphenoid and pterygoids, the question arises whether in these ancestral forms they did or did not reach the vomers.

On the other hand, it is possible that, in some manner yet to be discovered, the ancestral series of Terrestrial Vertebrata may have combined the characters of the later differentiated forms, as Gadow has surmised in his sagacious remark² that “the Amphibia and Reptiles do not form a continuous line of development, but are two divergent branches of a common stock of Palæozoic Tetrapoda.” If, with Credner, we group together the Stegocephalia and “Proganosauria” as the “Eotetrapoda”³, or with Dawson and Baur⁴ associate a no less heterogeneous assemblage under the cognomen “Microsauria,” we but imply the conviction herein set forth.

Concerning the phalangeal problem, the discovery that certain living Chelonia are hyperphalangeata⁵; that by Peters⁶ that in the Pleurodian Pelomedusa the numerical reduction of the phalanges is in part due to fusion of more numerous elements during

¹ Sewertzoff writes (Bull. Soc. Nat. Mosc. n. s. vol. ix. 1895, p. 186): “Bei die Amphibien entspricht der Ganze Occipitalabschnitt einem einzigen Segmente, dein einfachen Occipitalbogen, so dass die Amphibien in dieser Hinsicht unter allen Cranioten, mit Ausnahme der Petromyzonten, die einfachsten Zustand zeigen.” Intensely interesting in this association are the recent observations of Peter (*op. cit.* [*antea*, p. 50] pp. 590–592), based on the discovery in Ichthyophis of a postvagial nerve, having, it would seem, an essential similarity to the “spinal accessory” of the Amniota.

² Gadow, H.: Phil. Trans. vol. 187. 1896, p. 23.

³ Credner, H.: Allgem. Verstell. naturwiss. Abhandlg. Berlin, Hft. xv. 1891 (“Naturwiss. Wochenschr.”), pp. 1–52.

⁴ Cf. Baur, G.: Anat. Anz. Bd. xiv. 1897, p. 148, and Bd. xi. 1896, p. 657.

⁵ Cf. Boulenger, G. A.: Brit. Mus. Cat. Chelonians, 1889, p. 240, spec. Chitra.

⁶ Peters, W.: Reise nach Mossambique, Zool. iii. Berlin, 1882, p. 6.

ontogeny; the investigation of Kükenthal, which has brought to light the remarkable fact¹ that the fourth and fifth digits of the Crocodilian fore limb are developmentally hyperphalangate—all testify to the great potentiality of the digital blastema², and do away with the value of the mere numerical difference as a criterion of affinity.

The question thus resolves itself into this—are the Terrestrial Vertebrata the descendants of the afore-defined Batrachian-Reptilia or of Reptilian-Batrachia? The problem for the immediate future lies in the study of the occiput, the sternal skeleton, and the quadrate; and, to our thinking, *Sclerocephalus*, with its multisegmented and structurally simple “plastron,” its “fanged” vomer, its elongated dentigerous pterygoid³, and its quadrate, points the way.

It is certain, but most unfortunate, that in its earliest forms, the sternum, known to us only in its definitive conditions, was cartilaginous, and has been lost to us in the palæontological record. The discovery by Osborn, however, of a cartilaginous sternum in the fossil state⁴, gives us hope. The decision must lie with the future. Anatomist and palæontologist must approach the question in the spirit of a combined morphological brotherhood; and its solution will mark an epoch in the progress of the vertebrate morphology of the era of its discovery.

Addendum, Nov. 16, 1900.

Shortly after the proofs of this Memoir were revised for press, there reached us a recently published paper on the organogeny of *Sphenodon*, by Professor H. Schauinsland, of Bremen (*Archiv. Mikr. Anat.* Bd. lvi. pp. 447–867). Although it came to hand too late for comment in our pages, we observe from its perusal that it is in places erroneous, and that we should have lost nothing by its earlier appearance, since its author is insufficiently acquainted with the literature of the subject, and apparently ignorant of the recent important papers by Deudy, now more than a year old.

LIST OF THE MORE IMPORTANT MEMOIRS DEALING WITH SPHENODON.

- 83^a. ALBRECHT, P. Note sur la présence d'un Rudiment de Proatlas sur un exemplaire de *Hatteria punctata*. *Bull. Mus. Belg.* tom. ii. pp. 185–193. (First record of pro-atlas.)
- 83^b. —. Epiphyses osseuses sur les Apophyses épineuses des Vertèbres d'un Reptile (*Hatteria punctata*, Gray). *Bruzelles*, 1883. Pp. 1–6.
- 86^a. BAUR, G. Die zwei Centralia im Carpus von *Sphenodon* (*Hatteria*) und die Wirbel von *Sphenodon* und *Gecko verticillatus*, Laur. (*G. verus*, Gray). *Zool. Anz.* Bd. ix. pp. 188–190.

¹ Kükenthal, W.: *Morphol. Jahrb.* Bd. xix. 1893, p. 50.

² In a manner akin to that of the passing “jointing” of the hyoid cornu described in the text (*antea*, p. 48).

³ It is unfortunate that its parasphenoid is unknown, but it must assuredly have possessed one, and that probably dentigerous.

⁴ Osborn, H. F.: *op. cit.* *antea*, p. 14.

- 86^b. BAUR, G. Osteologische Notizen über Reptilien. *Zool. Anz.* Bd. ix. pp. 685-690. (Cf. Günther, *op. cit.* p. 746, and Baur, G., *ibid.* Bd. x. pp. 120-121.)
- 86^c. —. Osteologische Notizen über Reptilien. *Zool. Anz.* Bd. ix. pp. 733-743.
- 86^d. —. The Ribs of Sphenodon (Hatteria). *Amer. Natural.* vol. xx. pp. 979-981.
87. —. On the Morphology of Ribs. *Amer. Natural.* vol. xxi. pp. 942-945.
88. —. Osteologische Notizen über Reptilien. *Zool. Anz.* Bd. xii. pp. 40-47. (Parasphenoid, epipterygoid, and alisphenoid.)
89. —. Revision meiner Mittheilungen im Zoologischen Anzeiger mit Nachträgen. *Zool. Anz.* Bd. xii. pp. 238-243. (Quadratojugale and otic bones.)
91. —. The Lower Jaw of Sphenodon. *Amer. Natural.* vol. xxv. pp. 489-490.
- 95^a. —. Ueber die Morphologie des Unterkiefers der Reptilien. *Anat. Anz.* Bd. xi. pp. 410-415.
- 95^b. —. Das Gebiss von Sphenodon (Hatteria) und einige Bemerkungen über Prof. Rud. Burckhardt's Arbeit über das Gebiss der Sauropsiden. *Anat. Anz.* Bd. xi. pp. 436-439.
84. BAYER, F. Ueber die Extremitäten einer jungen Hatteria. *Stzb. Akad. Wien*, Bd. xc. pp. 237-245.
87. BEMMELEN, J. F. Beiträge z. Kenntniss d. Halsgegend b. Reptilien. I. Anat. Theil. *Bijdr. t. d. Nied. Dierkd. Ver. Amsterdam*, 1887, pp. 102-146. (Contains an accurate account of nerves, blood-vessels and glands of neck of Sphenodon.)
94. BERG, J. Zur Kenntniss der Brückenechse. *Zool. Garten*, Bd. xxxv. pp. 102-105 and pp. 146-150. (An admirable figure of Sphenodon.)
89. BOULENGER, G. A. Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum, 1889, pp. 1-3.
91. —. On British Remains of Homœosaurus, with Remarks on the Classification of the Rhynchocephalia. *Proc. Zool. Soc.* 1891, pp. 167-172.
93. —. On some newly-described Jurassic and Cretaceous Lizards and Rhynchocephalians. *Ann. & Mag. Nat. Hist.* (ser. 6) vol. xi. pp. 204-210.
76. BULLER, W. L. Notes on the Tuatara Lizard (Sphenodon), with a Description of a supposed new Species (S. güntneri). *Trans. N. Zealand Inst.* vol. ix. pp. 317-325.
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98. BUSCH, C. H. Beiträge zur Kenntniss der Gaumenbildung bei den Reptilien. *Zool. Jahrb. (Anat. Abth.)* Bd. xi. pp. 441-499.
85. COLENZO, W. Notes on the Bones of a Species of Sphenodon (S. diversum, Col.) apparently distinct from the Species already known. *Trans. N. Zealand Inst.* vol. xviii. 1885, pp. 118-123.
86. COPE, E. D. The Intercentrum in Sphenodon. *Amer. Natural.* vol. xx. p. 175.
88. CORNET, J. Note sur le prétendu Pro-atlas des Mammifères et de Hatteria punctata. *Bull. Ac. Belgique (sér. 3)*, tom. xv. pp. 406-420.
98. DENDY, A. Summary of the principal Results obtained in a Study of the Development of the Tuatara (Sphenodon punctatus). *Proc. R. Soc.* vol. lxiii. pp. 440-443.
- 99^a. —. Outlines of the Development of the Tuatara (Sphenodon punctatus). *Quart. Journ. Micr. Sci.* vol. xlii. pp. 1-87.

- 99^b. DENDY, A. On the Development of the Parietal Eye and adjacent Organs in *Sphenodon*. *Ibid.* pp. 111-153.
- 99^c. —. The Life-History of Tuatara (*Sphenodon punctatus*). *Trans. N. Zealand Inst.* vol. xxxi. pp. 249-255.
99. DENDY, A., and HOWES, G. B. The Hatching of Tuatara Eggs. *Nature*, vol. lix. p. 340.
84. DOLLO, L. Notes Erpétologiques. *Zool. Anz.* Bd. vii. pp. 547-548. (First description of condylar foramina of humerus. More fully described with figures in *Bull. Mus. Belg.* tom. iii. p. 151). (Cf. also Fürbringer, *Morph. Jahrb.* Bd. xi. pp. 484-486.)
88. —. Sur le ProAtlas. *Zool. Jahrb. (Anat. Abth.)* Bd. iii. pp. 433-446.
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42. —. Descriptions of two hitherto unrecorded Species of Reptiles from New Zealand. *Zool. Miscell.* 1842, p. 72.
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- 98^c. —. Ueber die Stellung der *Hatteria punctata* in der Tierreihe. *Verhandlg. Anat. Gesellschaft*, 1898 (*Anat. Anz.* Bd. xiv., Suppl.), pp. 100-106.
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PLATE I.

EXPLANATION OF THE PLATES¹.

PLATE I.

SPHENODON PUNCTATUS.—VERTEBRAL COLUMN AND RIBS.

a., arch of the atlas; *a.*, body of atlas (odontoid peg); *c.c.*, caudal canal; *c.v.*, cartilaginous vertebra; *f.t.*, fibrous tissue; *h.a.*, accessory hypapophysis; *i.p.*, primary intercentrum; *i.p.*', median intercentrum; *i.p.*'', chevron-bone; *i.s.*, secondary intercentrum; *i.sg.*, interseptal segment; *my.*, myelon (spinal cord); *n.a.*, neural arch; *nc.*, notochord; *nc.e.*, chordal epithelium; *nc.s.*, chordal sheath; *n.p.*, intravertebral chordal plate; *n.p.*', intervertebral chordal plate; *n.sp.*, neural spine; *oc.c.*, occipital condyle; *o.v.*, osseous vertebra; *r.cd.*, caudal rib; *r.s.*, sacral rib; *r.t.*, trunk rib; *s.l.*, splitting lamina; *s.o.*, skeletogenous sheath; *t.a.*, interarticular tissue; *v.c.*, vesicula centralis.

- Fig. 1. *Stage P. Vertebral Column*:—Lateral longitudinal section at about the region of vertebrae 6–8. × 50.
- Fig. 2. *Stage P. The same*:—Median longitudinal section through the region of fig. 1. × 50.
- Fig. 3. *Stage P. The same*:—Transverse section through the intervertebral region of caudal segments 2–3. × 40.
- Fig. 4. *Stage P. The same*:—Section through a vertebral region—the 6th segment in front of fig. 3. × 40.
- Fig. 5. *Stage Q. Vertebral Column*:—Lateral longitudinal section in the region of vertebrae 20–23. × 40.
- Fig. 6. *Stage Q. The same*:—Median longitudinal section through vertebrae 20–23. × 40.
- Fig. 7. *Stage Q. The same*:—Longitudinal section (slightly oblique) through caudal vertebrae 3–6. × 40.
- Fig. 8. *Stage Q. The same*:—Median longitudinal section through the basi-occipital and the four anterior cervical vertebrae. × 40.
- Fig. 9. *Stage S. Vertebral Column*:—Longitudinal section through the basi-occipital and the three anterior cervical vertebrae. × 25.
- Fig. 10. *Stage S. The same*:—Median longitudinal section through vertebrae 13–15. × 25.
- Fig. 11. *Stage S. The same*:—Transverse section through the intervertebral region 5–6. × 25.
- Fig. 12. *Stage S. The same*:—Ventral aspect of the last presacral to the 9th caudal vertebrae showing free caudal ribs. × 5.
- Fig. 13. *Stage T. Vertebral Column*:—Median longitudinal section through vertebrae 7–10. × 18.
- Fig. 14. *Stage T. The same*:—Median longitudinal section through intercentrum 8–9 of fig. 13, showing minute structure. × 50.
- Fig. 15. *Adult. Vertebral Column*:—Median longitudinal section through vertebrae 9–11. × 11.
- Fig. 16. *Adult. The same*:—Ventral aspect of the 10th to the 20th vertebrae showing an abnormal condition of the intercentra. $\frac{3}{4}$ nat. size.
- Fig. 17. *Adult. The same*:—Median longitudinal section at about the region of the 12th caudal vertebra. × 5.
- Fig. 18. *Adult. The same*:—Caudal vertebrae 7–12 from the left side. $\frac{3}{4}$ nat. size.
- Fig. 19. *Adult. The same*:—Transverse section through plane *a-b* of fig. 17. × 11.
- Fig. 20. *Adult. The same*:—Caudal vertebra 11 from the left side. $\frac{3}{4}$ nat. size.
- Fig. 21. *Adult. The same*:—Caudal vertebrae. $\frac{3}{4}$ nat. size.

¹ In all the Plates, where colouring has been employed, blue indicates hyaline cartilage and yellow bone, with the exception of Pl. I, fig. 13.

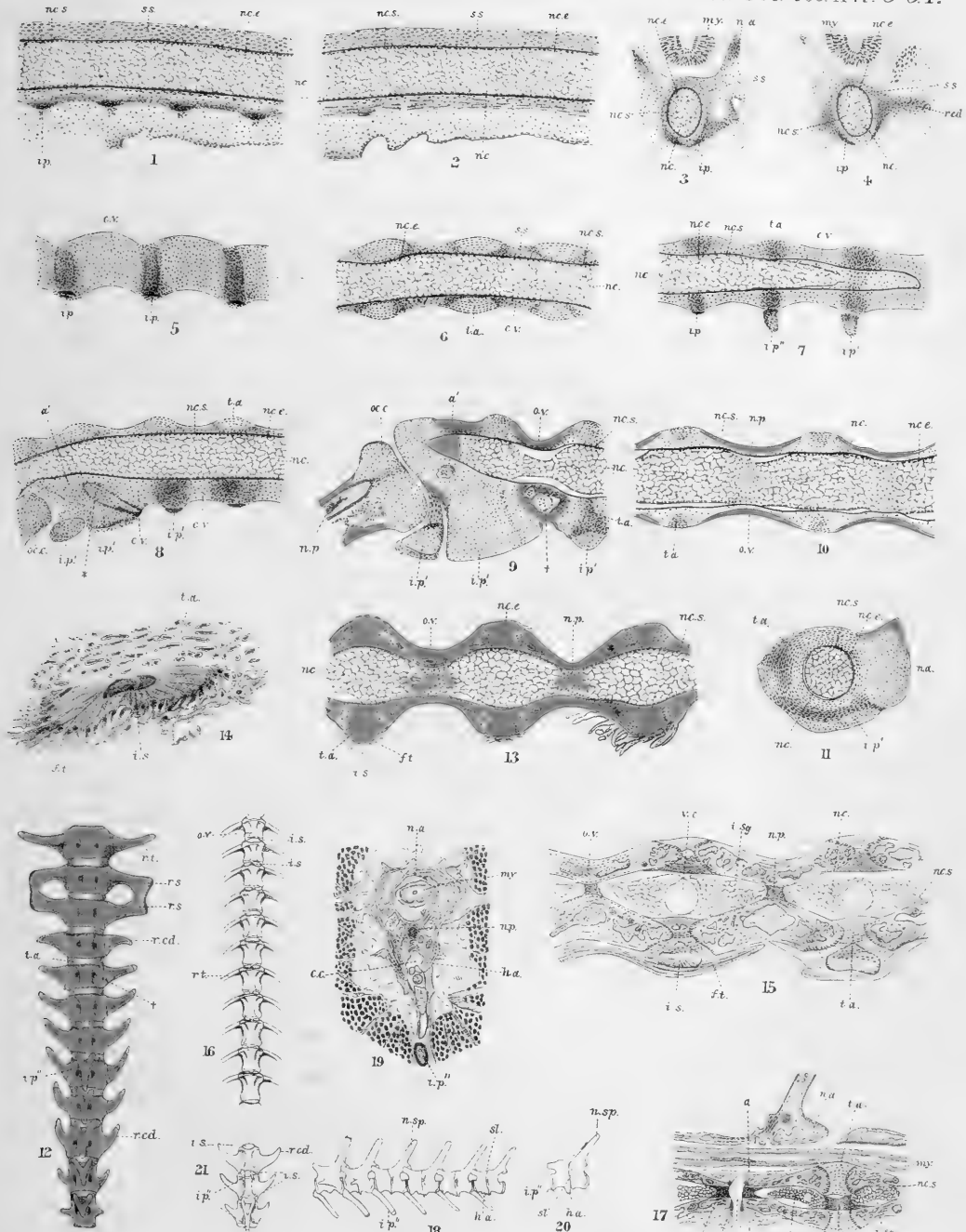


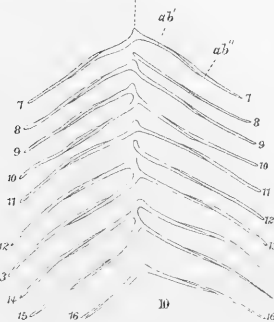
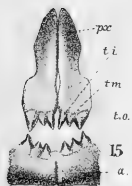
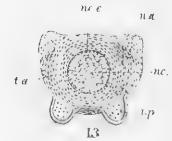
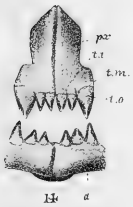
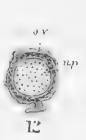
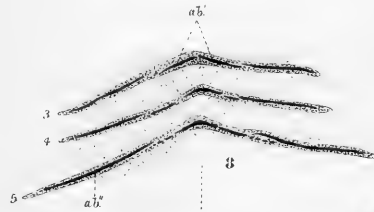
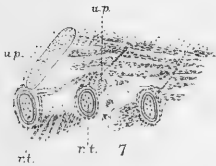
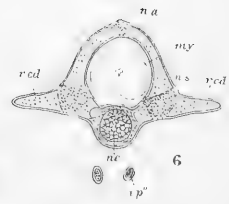
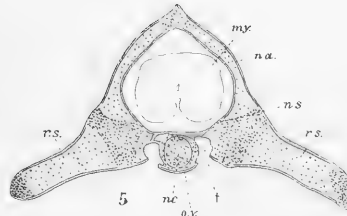
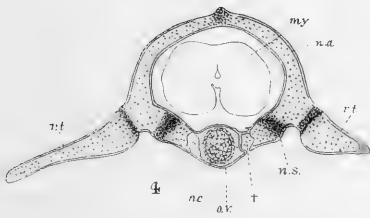
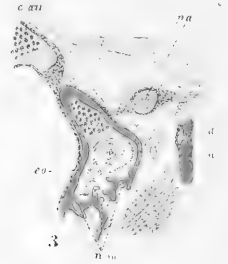
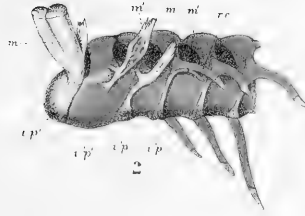
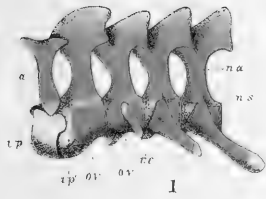
PLATE II.

PLATE II.

SPHENODON PUNCTATUS.—VERTEBRAL COLUMN AND RIBS, GASTRALIA, AND TEETH.

a., arch of atlas; *ab.*^l, abdominal rib, median portion; *ab.*^h, abdominal rib, lateral portion; *c.au.*, auditory capsule; *d.*, dentary; *e.o.*, exoccipital; *g.t.*, gastralia tissue tracts; *i.p.*^l, median intercentrum; *i.p.*^h, chevron-bone; *m.*, costo-cervical muscle; *m.*^l, ligament of costo-cervical muscle; *mk.*, Meckel's cartilage; *mx.*, maxilla; *my.*, myelon (spinal cord); *n.*^l, first spinal nerve; *n.xii.*, twelfth cranial nerve; *n.a.*, neural arch; *nc.*, notochord; *nc.e.*, chordal epithelium; *nc.s.*, chordal sheath; *n.p.*, intravertebral chordal plate; *n.s.*, neurocentral suture; *o.v.*, ossaceous vertebra; *p.a.*, pro-atlas; *p.x.*, premaxilla; *r.c.*, cervical rib; *r.cd.*, caudal rib; *r.s.*, sacral rib; *r.t.*, trunk rib; *t.a.*, interarticular tissue; *t.ch.*, cheek-tooth; *t.d.*, developing tooth; *t.f.*, fully-formed tooth (fused with bone); *t.i.*, inner incisor; *t.m.*, middle incisor; *t.o.*, outer incisor; *t.p.*, transpalatine; *u.p.*, uncinat process.

- Fig. 1. *Stage S. Anterior cervical vertebrae*:—The first five vertebrae showing anterior cervical ribs, lateral aspect. × 8.
- Fig. 2. *Stage T. The same*:—The first 5-6 vertebrae showing osseous and so-called ligamentous cervical ribs from left side, ventro-lateral aspect. × 4.
- Fig. 3. *Stage S. The "Pro-Atlas"*:—Lateral longitudinal section, including the exoccipital. × 20.
- Fig. 4. *Stage S. The Ribs*:—Transverse section of last presacral vertebral segment. × 20.
- Fig. 5. *Stage S. The same*:—Transverse section of the second sacral vertebral segment. × 20.
- Fig. 6. *Stage S. The same*:—Transverse section of the fourth caudal vertebral segment. × 20.
- Fig. 7. *Stage R. Uncinate process*:—Section through a poststernal rib showing development of uncinat process. × 25.
- Fig. 8. *Stage S. Abdominal ribs*:—Ventral aspect of ribs 3-5. × 8.
- Fig. 9. *Stage S. The same*:—Ventral aspect of ribs 16-18 of right side. × 11.
- Fig. 10. *Stage T. The same*:—Ventral aspect of ribs 7-16 showing irregular union of parts. × 2.
- Fig. 11. *Stage R. Notochordal plate*:—Transverse section showing first origin. × 40.
- Fig. 12. *Stage S. The same*:—Transverse section at full formation. × 25.
- Fig. 13. *Stage S. Chevron-bones*:—Transverse section showing attachment to fourth caudal vertebra. × 25.
- Fig. 14. *Stage S. Incisor teeth*:—Front aspect. × 5.
- Fig. 15. *Stage T. The same*:—Front aspect. × 4.
- Fig. 16. *Stage T. The same*:—Median longitudinal section through second upper incisor and associated parts. × 23.
- Fig. 17. *Stage T. Maxillo-palatine teeth*:—Combined drawing—the teeth already confluent with the bone being indicated in outline, the developing teeth in colour. × 13.
- Fig. 18. *Stage S. Check-tooth*:—Transverse section, including dentary and Meckel's cartilage. × 20.



II ILS del
M P, Parker lith

SPHENODON PUNCTATUS
Vertebral Column & Ribs, Gastralia & Teeth.

Geo West L. Sons imp

PLATE III.

PLATE III.

SPHENODON PUNCTATUS.—DEVELOPING SKULL, EARLIER STAGES.

The figures on this Plate are of wax models reconstructed from microscopic sections, the skeletal parts being alone represented. The fenestræ and interspaces in the chondrocranium are for the most part occupied by membrane (not indicated), except in so far as they transmit nerves and blood-vessels (*cf.* Pl. IV. fig. 10).

an., angular; *ar.*, articular; *b.s.*', basipterygoid process; *c.*', anterior semicircular canal; *c.au.*, auditory capsule; *c.r.*, coronoid; *d.*, dentary; *e.c.*, extrastapedial cartilage; *e.n.*, external nares; *e.o.*, exoccipital; *epg.*, epipterygoid; *e.s.*, ethmosphenoidal plate; *ex.*, extranasal; *ex.*¹⁻⁴, extranasal processes; *f.i.-xii.*, foramina for exit of cranial nerves; *f.a.*, foramen for ophthalmic branch of the carotid; *f.e.*, ethmoidal foramen; *f.i.*, interorbital fenestra; *f.j.*, foramen for jugular vein; *f.m.*, foramen magnum; *f.n.*, lateral cranial fenestra; *fr.*, frontal; *h.*, hyoid; *h.*', anterior cornu of the hyoid; *h.*', posterior cornu of the hyoid; *i.n.*, internal nares; *j.*, jugal; *mk.*, Meckel's cartilage; *mx.*, maxilla; *mx.*', maxillary process; *n.a.p.*, alinasal process; *nc.*, notochord; *n.c.*, nasal capsule; *n.c.*', supranasal process; *n.c.*', prenasal process; *nf.*', nasal fenestra; *n.pa.p.*, nasopalatine process; *n.p.p.*, naso-premaxillary process; *ns.*, nasal; *n.v.p.*, inferior naso-vomerine process; *oc.c.*, occipital condyle; *os.*, otosphenoidal plate; *os.*¹⁻⁵, otosphenoidal processes; *p.*, parietal; *pa.*, palatine; *par.*, parachordal; *p.f.*, prefrontal; *pg.*, pterygoid; *pg.*', pterygoid process; *p.o.*, postorbital; *po.f.*, postfrontal; *p.p.*, parotic process; *p.q.*, pterygo-quadrato; *ps.*, presphenoidal cartilage; *p.s.*, parasphenoid; *px.*, premaxilla; *py.*', pituitary foramen; *q.*, quadrato; *q.*', otic process of quadrato; *q.j.*, quadrato-jugal; *s.a.*, supra-angular; *sb.*, subnasal; *s.i.*, interorbital septum; *s.mx.*, septo-maxillary; *s.o.*', supraoccipital cartilage; *sp.*, splenial; *sq.*, squamosal; *sq.*', posterior process of squamosal; *s.st.*, suprastapedial cartilage; *st.*, stapes; *tp.*, transpalatine; *tr.*, trabecula; *vo.*, vomer.

- Fig. 1¹. Stage P. Developing chondrocranium:—Left lateral aspect. The arrow indicates the direction of the longitudinal axis of the embryo as it lay coiled. × 13.
 Fig. 2¹. Stage P. The same:—Ethmoidal, trabecular, and sphenoidal regions, dorsal aspect. × 13.
 Fig. 3¹. Stage P. The same:—Parachordal and auditory regions, dorsal aspect. × 13.
 Fig. 4. Stage Q. Developing chondrocranium:—Lateral aspect. × 8.
 Fig. 5. Stage Q. Developing skull:—Lateral aspect. × 8.
 Fig. 6. Stage Q. Developing chondrocranium:—Ventral aspect. × 8.
 Fig. 7. Stage Q. The same:—Dorsal aspect. × 8.
 Fig. 8. Stage R. Developing chondrocranium:—Lateral aspect. × 8.
 Fig. 9. Stage R. Developing skull:—Posterior aspect. × 8.
 Fig. 10. Stage R. The same:—Lateral aspect. × 8.
 Fig. 11. Stage R. The same:—Dorsal aspect. × 8.
 Fig. 12. Stage R. The same:—Ventral aspect. × 8.

¹ In these figures the uncoloured areas represent pro-cartilage.

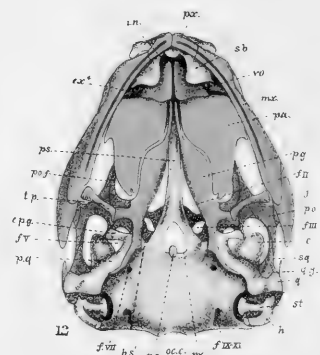
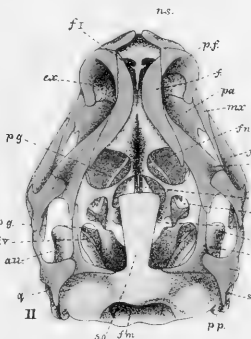
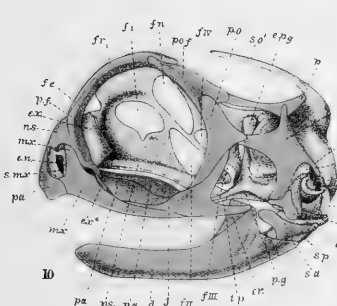
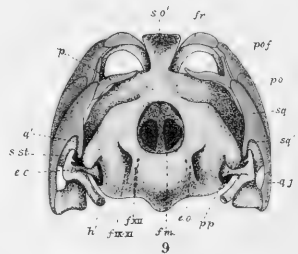
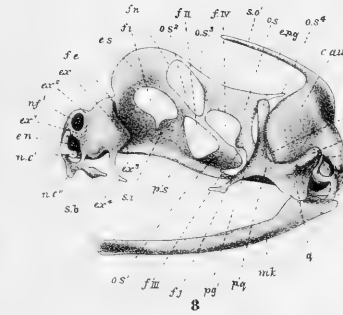
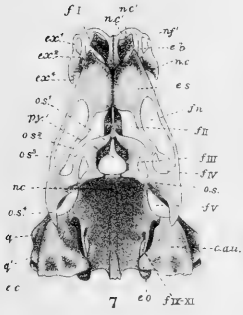
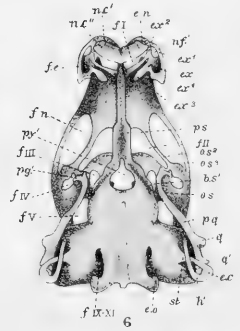
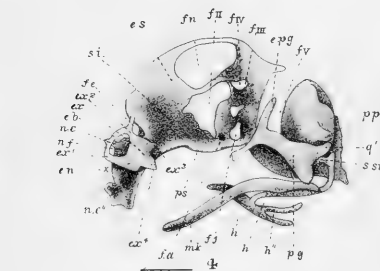
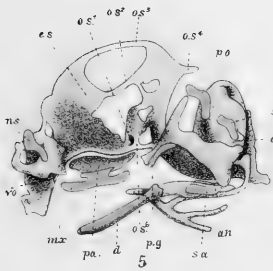
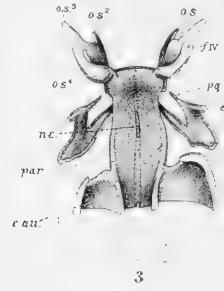
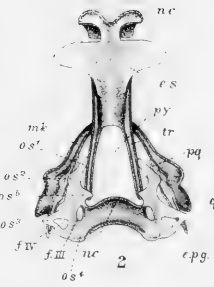
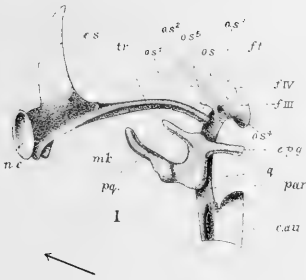




PLATE IV.

PLATE IV.

SPHENODON PUNCTATUS.—DEVELOPING SKULL, LATER STAGES.

an., angular; *ar.*, articular; *b.o.*, basi-occipital; *b.s.*, basisphenoid; *b.s.*¹, basipterygoid process; *c.*¹, anterior semicircular canal; *c.*², posterior semicircular canal; *cr.*, coronoid; *d.*, dentary; *e.c.*, extrastapedial cartilage; *e.n.*, external nares; *e.o.*, exoccipital; *e.p.g.*, epipterygoid; *e.s.*, ethmosphenoidal plate; *ex.*, extranasal; *ex.*¹—*ex.*⁵, extranasal processes; *f.i.-xii.*, foramina for exit of cranial nerves; *f.*, fenestra in the suprastapedial cartilage; *f.e.*, ethmoidal foramen; *f.i.*, interorbital fenestra; *f.j.*, foramen for jugular vein; *f.n.*, fenestra in the anterior wall of the brain-case; *f.p.*, parietal foramen; *fr.*, frontal; *h.*¹, anterior cornu of the hyoid; *i.n.*, internal nares; *j.*, jugal; *l.d.*, lachrymal duct; *mk.*, Meckel's cartilage; *mp.*, meniscus pterygoideus; *mx.*, maxilla; *mx.*¹, maxillary process; *n. v.*, *vi.*, cranial nerves; *n.c.*, nasal capsule; *n.c.*¹, supranasal process; *n.c.*², prenasal process; *nf.*¹, *nf.*², nasal fenestræ; *ns.*, nasal; *oc.c.*, occipital condyle; *op.*, opisthotic; *o.s.*, otosphenoidal plate; *o.s.*¹—*o.s.*⁴, otosphenoidal processes; *p.*, parietal; *pa.*, palatine; *p.f.*, prefrontal; *p.g.*, pterygoid; *p.g.*¹, pterygoid process; *p.o.*, postorbital; *po.f.*, postfrontal; *p.p.*, parotic process; *pro.*, prootic; *ps.*, presphenoidal cartilage; *p.s.*, parasphenoid; *px.*, premaxilla; *py.*, pituitary body; *q.*, quadrate; *q.*¹, otic process of quadrate; *q.j.*, quadrato-jugal; *s.a.*, supraangular; *sb.*, subnasal; *s.i.*, interorbital septum; *s.mx.*, septo-maxillary; *s.o.*, supra-occipital; *s.o.*¹, supra-occipital cartilage; *sp.*, splenial; *sq.*, squamosal; *sq.*¹, anterior process of squamosal; *sq.*², posterior process of squamosal; *s.st.*, suprastapedial cartilage; *st.*, stapes; *t.p.*, transpalatine; *vo.*, vomer.

- Fig. 1. *Stage R-S. The head* :—Transverse section through epipterygoid region (γ - δ of fig. 4). × 6.
- Fig. 2. *Stage R-S. The same* :—Combined figure of two transverse sections through the nasal region (α - β of fig. 4), the left half several sections in front of the right. × 15.
- Fig. 3. *Stage R-S. The same* :—Transverse sections showing detailed relations of pterygoid and basisphenoid (seven sections in front of fig. 1). × 18.
- Fig. 4. *Stage S. Developing skull* :—Lateral aspect. × 5.
- Fig. 5. *Stage S. The same* :—Dorsal aspect. × 5.
- Fig. 6. *Stage S. The same* :—Ventral aspect. × 5.
- Fig. 7. *Stage S. The same* :—Posterior aspect. × 5.
- Fig. 8. *Stage T. Developing skull* :—Dorsal aspect. × 3.
- Fig. 9. *Stage T. The same* :—Posterior aspect. × 3.
- Fig. 10. *Stage T. The chondrocranium* :—With endostoses and the parasphenoid; as seen after removal of the mandibular skeletal arch. Left lateral aspect. × 3.
- Fig. 11. *Stage T. The left pterygo-quadrate arch and squamosal* :—Lateral aspect. × 5.

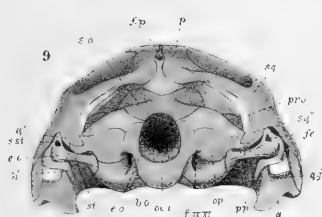
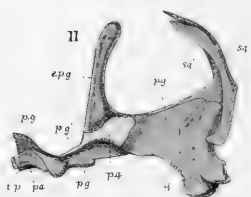
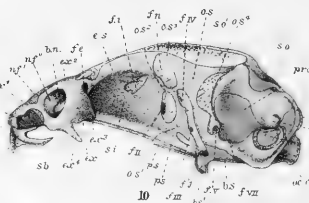
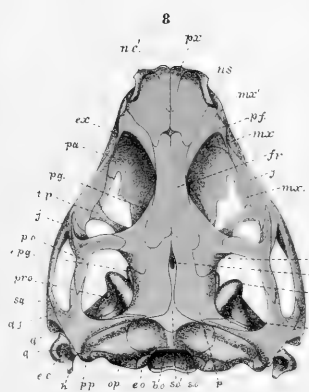
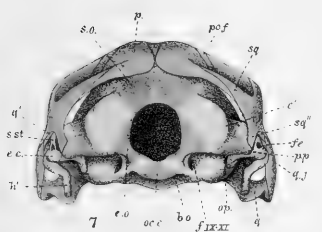
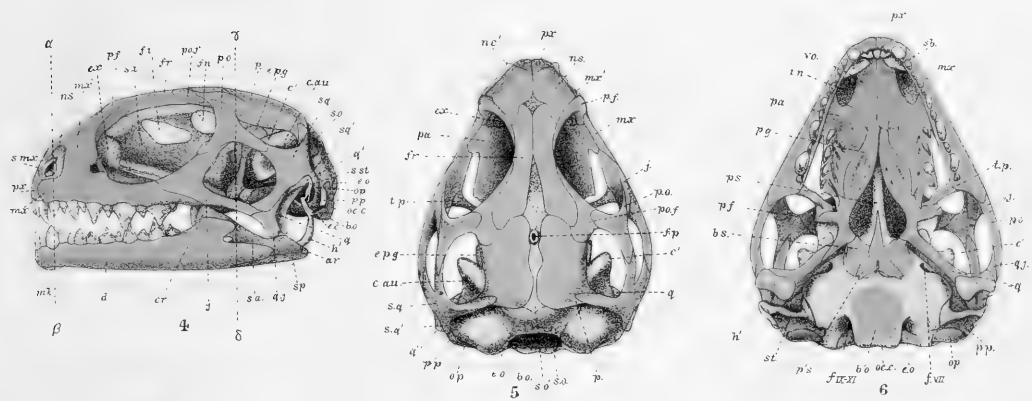
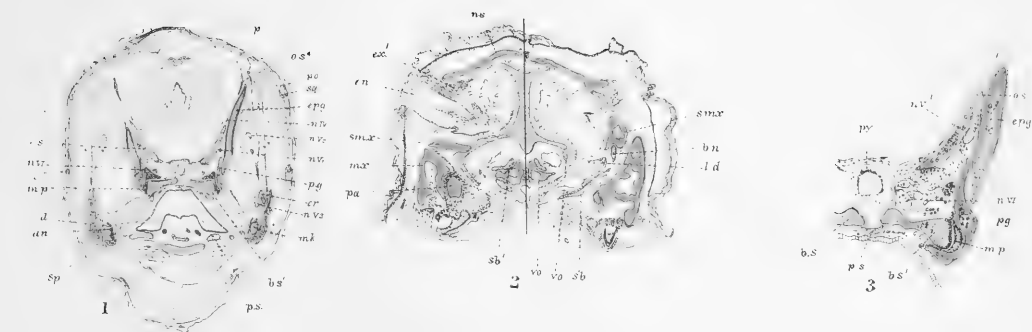




PLATE V.

PLATE V.

SPHENODON PUNCTATUS.—THE QUADRATE, HYOID, AND COLUMELLA AURIS.

an., angular; *b.*, boundary between stapes and extrastapedial cartilage; *b.a.*, branchial arch; *b.c.*, branchial cleft; *c.^{III}*, horizontal semicircular canal; *ca.*, carotid artery; *ca.^I*, branch of carotid artery; *c.au.*, auditory capsule; *e.c.*, extrastapedial cartilage; *eu.*, eustachian recess; *fe.*, fenestra in suprastapedial cartilage; *h.^I*, anterior cornu of the hyoid; *j.v.*, jugular vein; *mk.*, Meckel's cartilage; *mt.*, mouth; *n. v.-xi.*, cranial nerves; *n. vii.^I*, branch of chorda tympani; *ph.*, pharynx; *p.p.*, parotic process; *pq.*, pterygoquadrate; *q.*, quadrate; *q.^I*, otic process of quadrate; *s.a.*, supraangular; *sq.^I*, anterior process of squamosal; *sq.^{II}*, posterior process of squamosal; *s.st.*, suprastapedial cartilage; *st.*, columella (stapes); *st.^I*, boundary between columella and extrastapedial cartilage.

Figs. 1-5. *Stage P.* A series of sections, in order from within outwards, showing the primary relationships of the columella auris to the hyoid and quadrate. × 40.

Fig. 1. Represents the most internal section No. 1.

Fig. 2. Represents section No. 6.

Fig. 3. " " No. 8.

Fig. 4. " " No. 19.

Fig. 5. " " No. 27.

Figs. 6-11. *Stage Q.* A similar series to the above. × 25.

Fig. 6. Represents the most internal section No. 1.

Fig. 7. Represents section No. 11.

Fig. 8. " " No. 26.

Fig. 9. " " No. 36.

Fig. 10. " " No. 46.

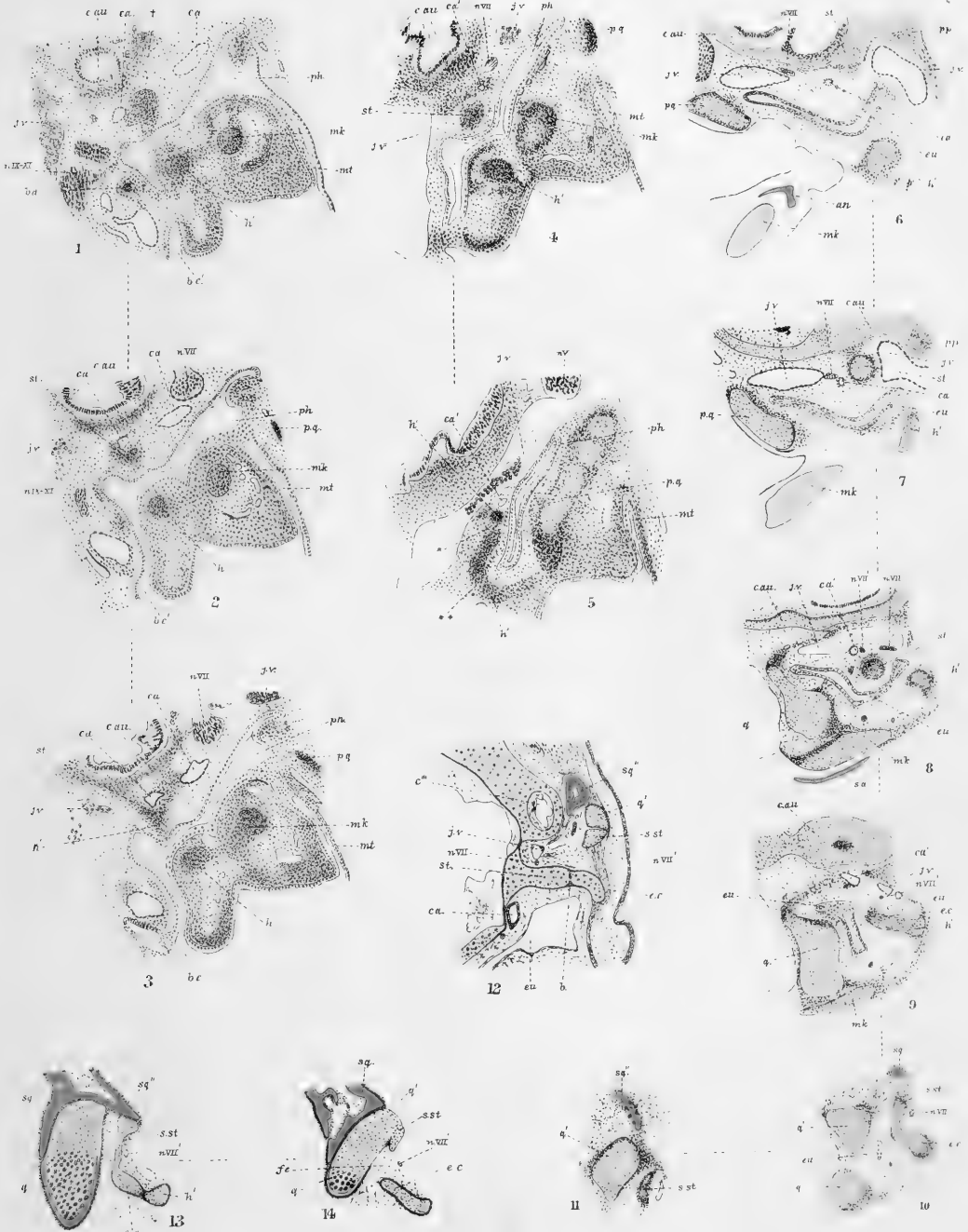
Fig. 11. " " No. 57.

Fig. 12. *Stage R.* Transverse section of auditory region passing through quadrate and columella auris. × 25.

Figs. 13-14. *Stage S.* Sections, in the same order as figs. 1-5, showing the relation of the suprastapedial cartilage to the quadrate. × 20.

Fig. 13. Represents the more internal section No. 1.

Fig. 14. Represents section No. 16.



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M.P. Parker lith.

Gen. West & Sons imp.

SPHENODON PUNCTATUS.
The Quadrate, Hyoid, & Columella auris



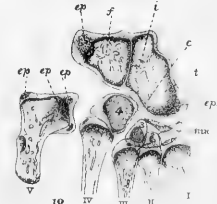
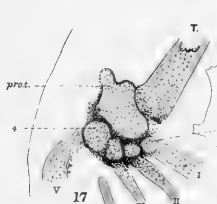
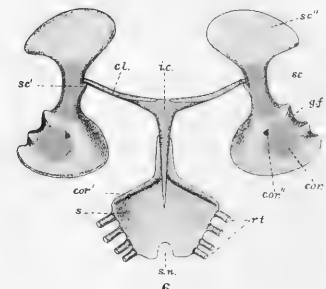
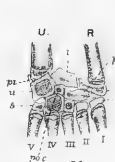
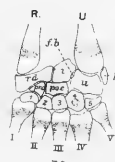
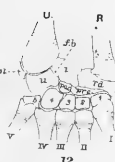
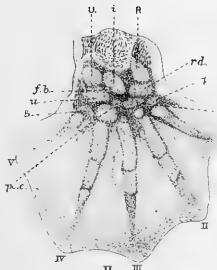
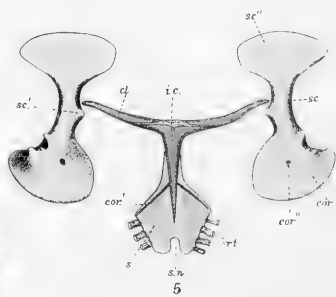
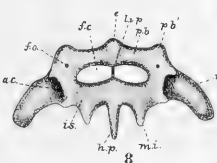
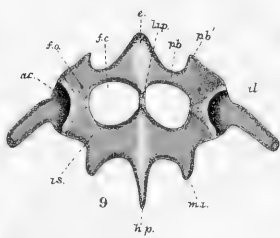
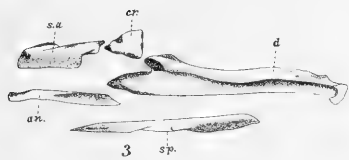
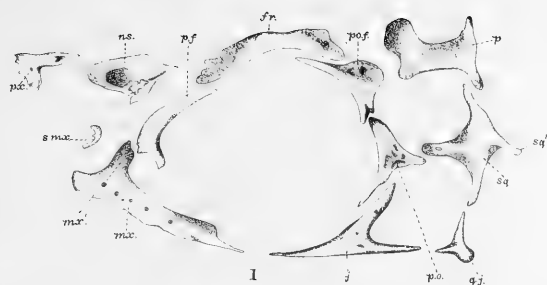
PLATE VI.

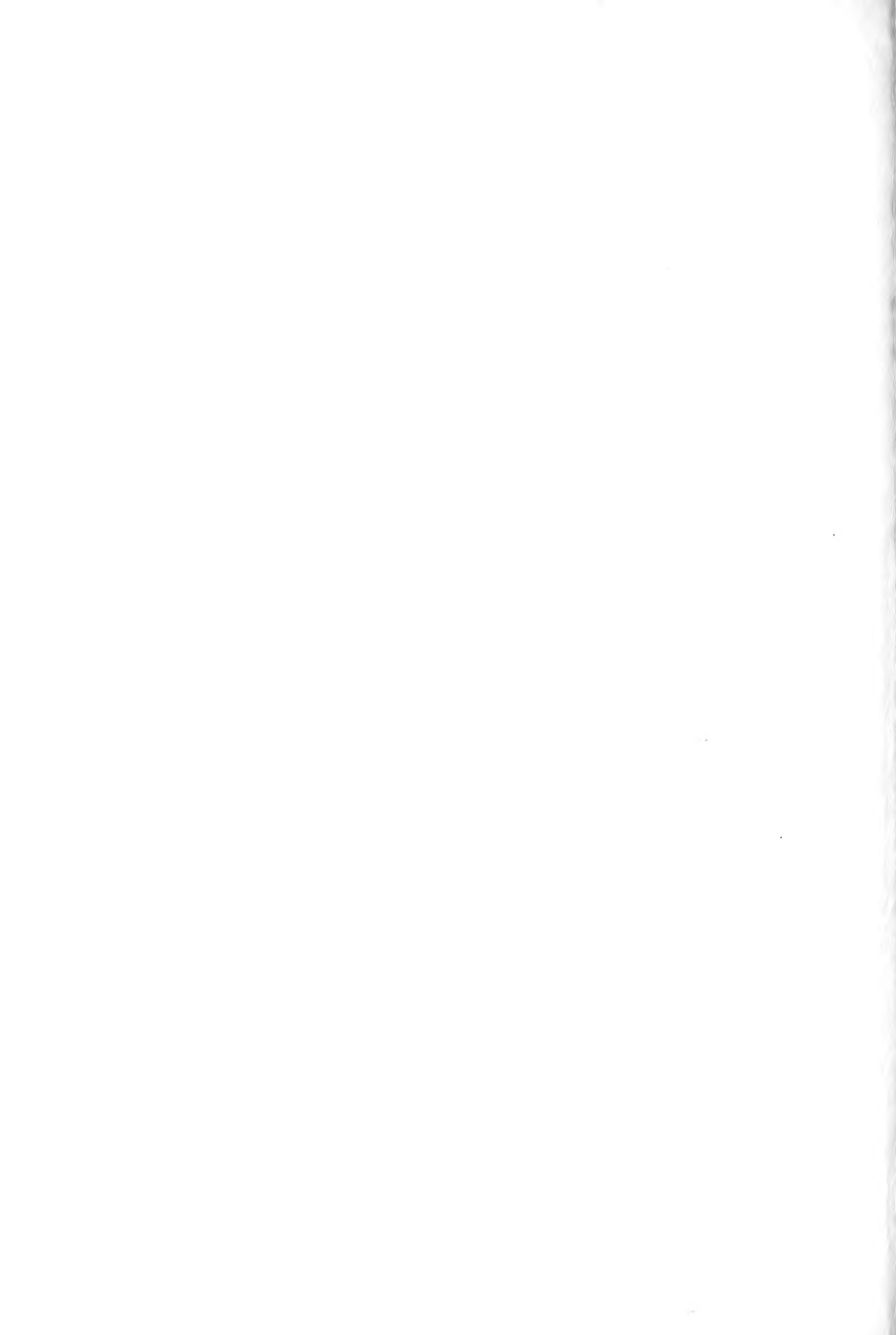
PLATE VI.

SPHENODON PUNCTATUS.—CRANIO-FACIAL MEMBRANE-BONES AND APPENDICULAR SKELETON.

ac., acetabulum; *an.*, angular; *c.*, centrale; *c.i.p.*, ischio-pubic cartilage; *cl.*, clavicle; *cor.*, coracoid; *cor.^l*, sulcus coracoideus; *cor.ⁿ*, foramen for supracoracoideus nerve; *d.*, dentary; *e.*, epipubis; *ep.*, epiphysis; *F.*, fibula; *f.*, fibulare; *f.b.*, foramen for arteria perforans mesopodii; *f.c.*, foramen cordiforme; *f.ec.*, ectepicondylar foramen; *f.en.*, entepicondylar foramen; *f.o.*, obturator foramen; *fr.*, frontal; *gf.*, glenoid fossa; *hp.*, hypoischium; *i.*, intermedium; *i.c.*, interclavicle; *il.*, ilium; *is.*, ischium; *j.*, jugal; *i.i.p.*, ischio-pubic ligament (ligamentum medianum pelvis); *m.i.*, metischial process; *mn.*, meniscus tarsale; *mx.*, maxilla; *mx.^l*, maxillary process; *ns.*, nasal; *p.*, parietal; *pa.*, palatine; *pb.*, pubis; *pb.^l*, prepubic process; *p.f.*, prefrontal; *pg.*, pterygoid; *pi.*, pisiform; *p.o.*, postorbital; *po.c.*, postaxial centrale; *po.f.*, postfrontal; *pr.c.*, preaxial centrale; *pro.t.*, proximal tarsal; *px.*, premaxilla; *q.j.*, quadrato-jugal; *R.*, radius; *rd.*, radiale; *r.t.*, trunk rib; *s.*, sternum; *s.a.*, supra-angular; *sc.*, scapula; *sc.^l*, acromial process; *sc.ⁿ*, suprascapula; *se.*, sesamoid; *s.mx.*, septo-maxillary; *s.n.*, poststernal notch; *sp.*, splenial; *sq.*, squamosal; *sq.^l*, posterior process of squamosal; *T.*, tibia; *t.*, tibiale; *t.c.*, tarsal centrale; *t.p.*, transpalatine; *U.*, ulna; *u.*, ulnare; *vo.*, vomer; I.-V., metacarpals and metatarsals; 1-5, carpals and tarsals.

- Fig. 1. *Stage S. The membrane-bones*:—Bones from roof of skull and side of head. × 5
 Fig. 2. *Stage S. The same*:—Bones from roof of mouth. × 5.
 Fig. 3. *Stage S. The same*:—Bones from lower jaw. × 5.
 Fig. 4. *Stage Q. Pectoral girdle and sternum*:—Longitudinal section with developing clavicle. × 25.
 Fig. 5. *Stage R. Pectoral girdle and sternum*:—Ventral aspect. × 8.
 Fig. 6. *Stage T. Pectoral girdle and sternum*:—Ventral aspect. × 2.
 Fig. 7. *Stage Q. Pelvic girdle*:—Ventral aspect (from wax model). × 8.
 Fig. 8. *Stage R. Pelvic girdle*:—Ventral aspect. × 5.
 Fig. 9. *Stage T. Pelvic girdle*:—Ventral aspect. × 2.
 Fig. 10. *Stage Q. Humerus*:—Distal end, ventral aspect (from wax model). × 15.
 Fig. 11. *Stage Q. Right carpus*:—Horizontal section. × 20.
 Fig. 12. *Stage T. Right carpus*:—Dorsal aspect, showing normal condition of centralia. × 4.
 Fig. 13. *Stage T. Left carpus*:—Dorsal aspect, showing abnormal condition of centralia from same animal as fig. 10. × 4.
 Fig. 14. *Small Adult. Right carpus*:—Dorsal aspect. × 2.
 Fig. 15. *Stage Q. Left tarsus*:—Early period, horizontal section. × 20.
 Fig. 16. *Stage Q. Right carpus*:—Late period, horizontal section. × 20.
 Fig. 17. *Stage R. Left tarsus*:—Horizontal section. × 15.
 Fig. 18. *Adult. Right tarsus*:—Dorsal aspect. × 2.
 Fig. 19. *Adult. Portion of left tarsus*:—Dorsal aspect, showing ulnar sesamoid. × 2.





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